FINAL REPORT TO

THE NATIONAL PARK SERVICE-COLORADO STATE UNIVERSITY

COOPERATIVE STUDIES UNIT

GRANT: CX-1200-2-BO48

VEGETATIONAL HISTORY OF ROCKY MOUNTAIN NATIONAL PARK: A FACTUAL PERSPECTIVE AS AN AID TO FOREST MANAGEMENT

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INTRODUCTION

There has been a surprising lack of paleoenvironmental research in Colorado (Nichols, 1982) and this has implications for the management of environmental problems in the public domain. The principal question addressed by our study concerns whether or not the current subalpine ecosystem boundaries are in equilibrium with modern climate, or whether they owe some part of their present distribution to past conditions which no longer exist, and are therefore unusually vulnerable to contemporary damage. If the upper treeline is stable or moving upslope, there will be a natural healing of human or natural damage (fires, felling, etc.). By contrast, if alpine treeline is falling, then any damage to the upper treeline will have difficulty in healing naturally.

The first major paleoenvironmental study in the Holocene for the Colorado Front Range was by Maher (1972) who restudied a site, Redrock Lake in the Brainard Valley, initially analyzed by Pennak, 1963; Redrock Lake is located 45 km south of Rocky Mountain National Park. This pioneering study drew on Maher's experience in sampling modern surface pollen deposition to form analogs for contemporary pollen and vegetational assemblages in the Holocene sediments. He stressed the use of ratios of spruce to pine pollen to estimate the apparent elevational distance of the sediment site from alpine treeline. Similar ratios of _Picea_ (spruce) and _Pinus_ (pine) can be found both below treeline and in the alpine (Maher, 1972: Fig. 6), a source of possible confusion.

The interpretation of Holocene events that Maher offers has been described by Nichols (1982) as being in antiphase (but with similar timing) to much of the rest of the North American climatic reconstructions. Perhaps most

important for our study is the lack of a mid-Holocene warm period; Maher interpreted the period from 6700 to 3000 BP as cooler than present while the period from 3000 BP to the present was said to have experienced higher treeline due to warmer summer climate.

COLLECTIONS

In Rocky Mountain National Park, collections have been made of the modern pollen "rain", subfossil wood remnants, and fossil peat and lake sites for pollen and insect remains. These are illustrated in Figure 1.

Modern Pollen Collections

Short collected moss and lichen polsters (i.e., small clumps of growing material which are commonly used as collectors of the modern pollen fallout) at 13 sites along a transect following Trail Ridge Road. Forty-three polsters were collected at these locations at elevations ranging from 8900' (2710 m) to 12,160' (3700 m) (Table I). Pollen analyses of these samples will provide an important analog to the pollen spectra registered in the fossil sediments. Analyses have not been attempted for these samples because of time constraints. Modern pollen collections have, however, been made under the CULTER program on Niwot Ridge, Green Lakes Valley, and Brainard Lake Valley, and some data are available for comparison.

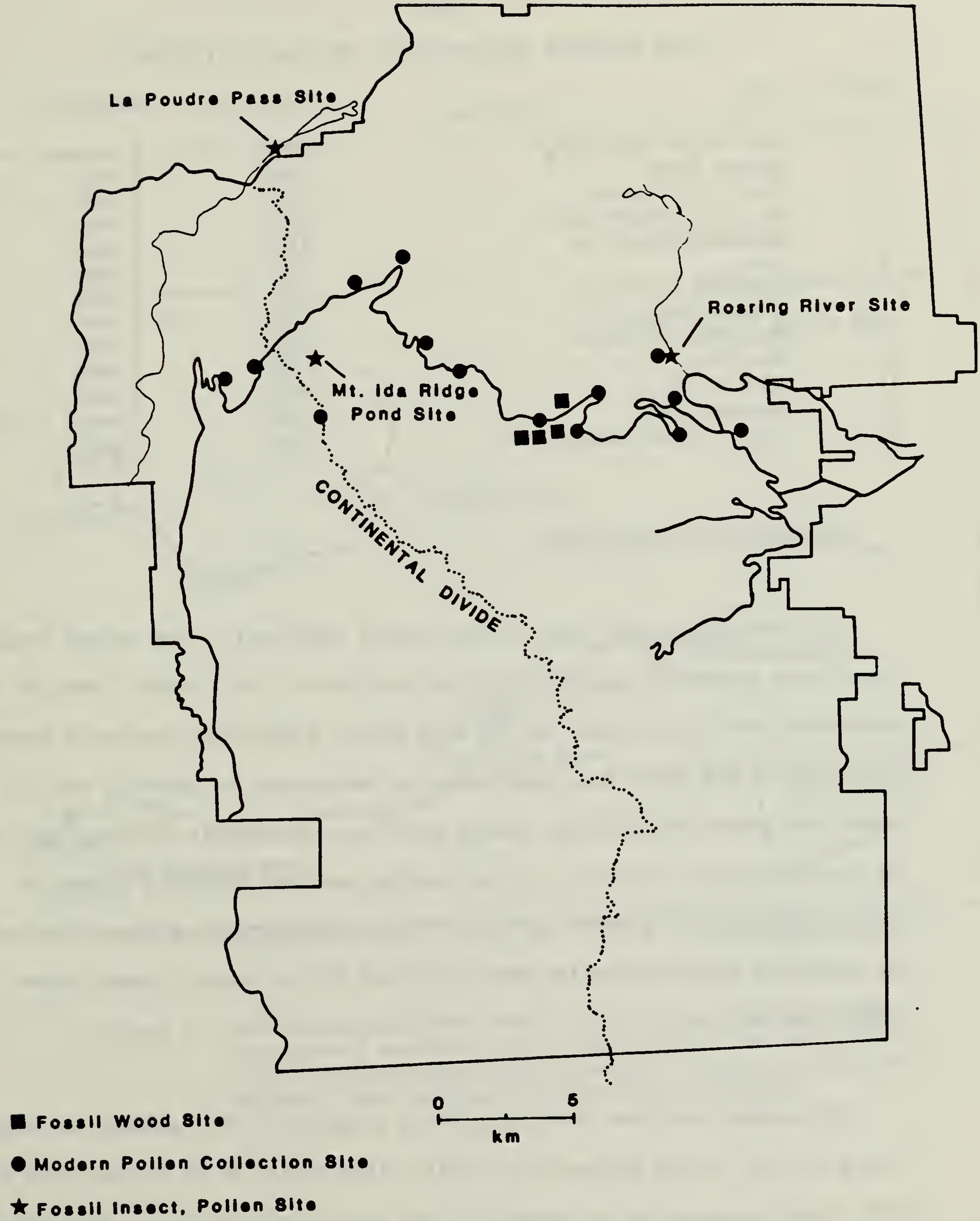

Figure 1. Map of Rocky Mountain National Park showing location of sampling sites, RMNP grant

TABLE I.

ROCKY MOUNTAIN NATIONAL PARK POLSTER COLLECTIONS

STOP #	SITE	ELEV. (m)	POLSTERS
1	Deer Ridge Junction	2720	3 lichen
2	Beaver Ponds	2790	3 moss
3	Many Parks Curve	2977	3 moss
4	Ski Lift Intersection	3195	4 moss
5	Rainbow Curve	3323	3 moss
6	Burn	3488	3 moss
7	Rock Cut	3707	3 moss
8	Iceberg Pass	3603	3 moss
9	Medicine Bow Curve	3537	3 moss
10	Treeline	3433	3 moss
11	Lake Irene	3232	3 moss
12	Phantom Creek	3048	2 moss, 1 lichen
13	Timber Creek Campground	2720	3 moss

Tree Stumps in the Alpine

The presence in the lower alpine zone of substantial tree stumps larger than living krummholz suggests that the treeline or the climatic limit of tree growth was previously higher by 100 m or more. Nichols has sampled a number of *in situ* stumps which have been dated by radiocarbon in order to help us understand recent vegetational events which are not clearly distinguished in the paleoecological record. All the samples are from dead tree stumps of *Picea engelmannii* (Englemann spruce) or *Abies lasiocarpa* (subalpine fir), with the outermost materials having been chiselled off to remove lichens, other organic matter, etc.

The samples are from Trail Ridge Road (Figure 1), Mt. Audobon, and also from Blue Lake in the Brainard Lake Valley (Figure 2), 45 km to the south of RMNP; these are detailed in Table II. The stumps have age ranges from 200 BP through 1700 BP, and suggest that present day conditions are not so favorable to tree growth in the lower alpine as they were formerly.

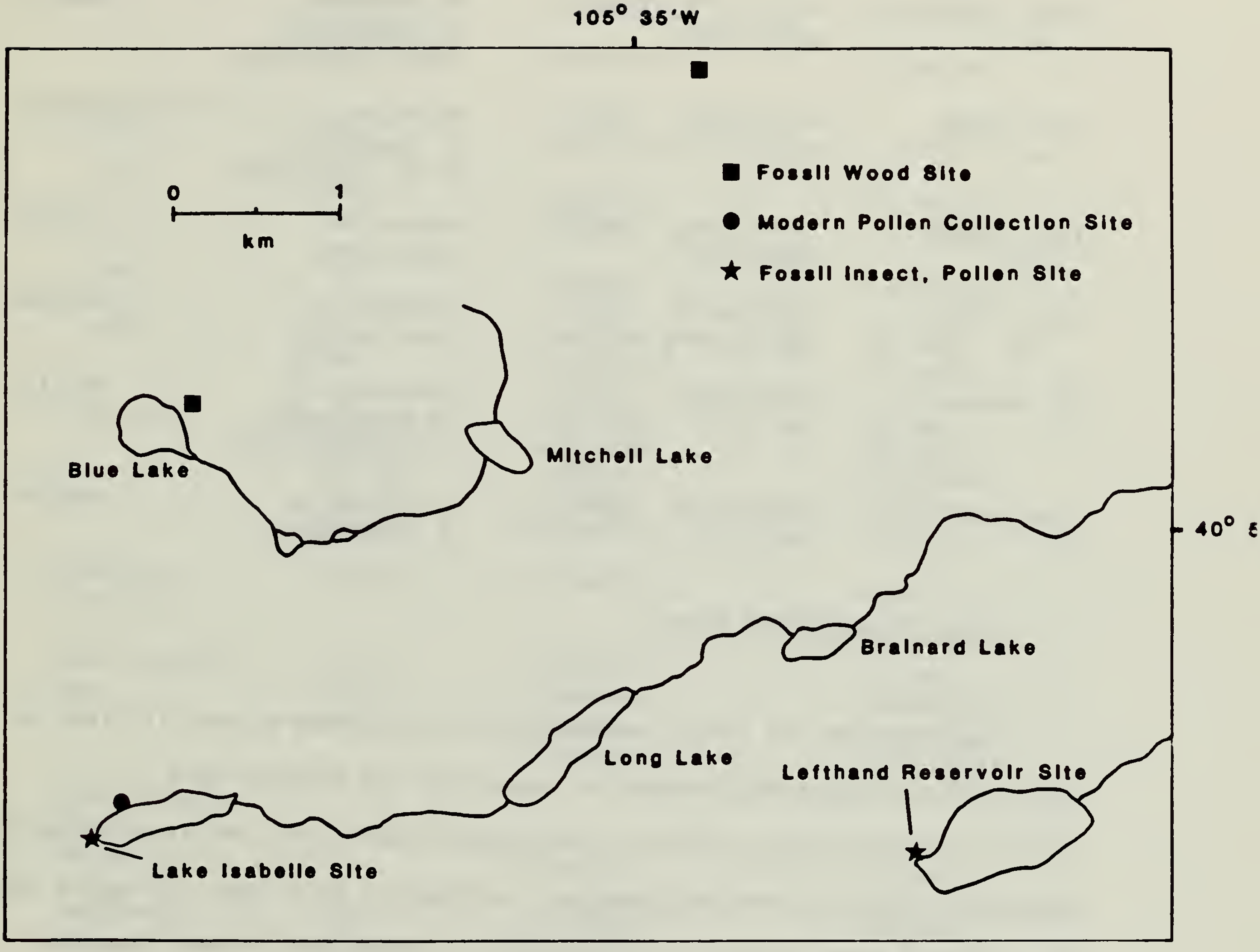

Figure 2. Map of Brainard Lake area, Colorado Front Range, showing location of sampling sites, RMNP grant. The location of LTER supported sites is also marked: Long Lake (pollen), Mitchell Lake (pollen), and Blue Lake (pollen).

TABLE II

ALPINE TIMBER SAMPLES, COLORADO FRONT RANGE

SITE	LOCATION	ELEV.(m)	MATERIAL	DATE(BP)
Trail Ridge #1	40°23'10"N, 105°41'30"W	3506	Heartwood of _P. englemannii_ or _A. lasiocarpa_	405±130
Trail Ridge #2	40°23'20"N, 105°41'25"W	3510	Heartwood of _P. engelmannii_ or _A. lasiocarpa_	340±125
Trail Ridge #3	40°23'20"N, 105°41'32"	3520	Branch of dead stump	215±130
Trail Ridge #4	40°23'54"N, 105°40'40"W	3450	Fragment of dead stump	1765±140
Mt. Audubon	40°07'03"N, 105°35'W	3490	Heartwood of _P. engelmannii_ or _A. lasiocarpa_	385±130
Blue Lake	40°06'24"N, 105°37'W	3450	Heartwood of _P. engelmannii_	200±125

Fossil Paleoecology Sites

Fossil pollen and insect remains have been examined in over 14 sites in the Colorado Front Range through the support of the National Park Service-Colorado State University Cooperative Studies Unit and also the CULTER (National Science Foundation) program. Analyses of four sites, La Poudre Pass Bog, Roaring River (organic detritus), Mt. Ida Pond, and Lefthand Reservoir Bog have been totally supported by this grant. Partial support has been provided for the Lake Isabelle Bog and delta sites. Three lake sites in the Brainard Lake area have been sampled through the CULTER program; pollen analyses are complete for Long Lake and Blue Lake (see Figure 1 and also Figure 2).

It is especially important to develop a well-controlled time frame for paleoecological studies; the ^{14}C dates received (Table III) provide a record dating back almost 12,000 years for the region.

TABLE III

RADIOCARBON DATES, RMNP AND CULTER STUDY

SITE	DEPTH (cm)	DATE (BP)	LAB NO.
Roaring River	0-12 (Level 1)	2400±130	GX-9613
	12-25 (Level 2)	2420±135	GX-9612
	Wood frags.	2350±140	GX-9614
La Poudre Pass			
LP-1	155	9850±300	W 4083
LP-3	54	5360±90	W 4826
	115	8810±90	W 4829
LP-5	5	1080±60	W 4830
LP-4	24-26	3485±180	GX-9998
	52-54	6360±210	GX-9999
Long Lake	20-25, 60-65	2880±150	SI-4950
	86-90	4035±170	GX-7707
	170-185	1910±80	SI-4949*
	265-285	9855±300	SI-4948
	285-290	11,800+450	GX-7723
Lefthand Reservoir	205-206	7760±160	DIC-1338
Lake Isabelle Bog	16-18	1495±130	GX-9684
	70-72	3280±195	GX-10629
	85-95	7080±90	SI-5646B**
		6390±90	SI-5746A**
Lake Isabelle Delta Section 1		6315±70	SI-5247
Section 2	0-6	7975±260	GX-10043
	35-40	7840±255	GX-10044
	81-98	9000±285	GX-10090
Mitchell Lake	40-50	6485±90	SI-5245
	397-417	10,920±360	SI-5189
Blue Lake	50-60	3190±185	GX-8938
	127-132	5680±370	GX-8937
	167-177	7840±370	SI-5244
	"240-250"	8055±310	GX-10387
Mt. Ida Ridge	1-6	4600±210	GX-10237
	25-30	8340±310	GX-10091
	50-55	9070±175	GX-9997

*Anomalous date; **A = > 125 μm screen fraction
**B = < 125 μm screen fraction

RESULTS

Roaring River

The catastrophic dam failure at Lawn Lake, Rocky Mountain National Park (Figure 1) on July 15, 1982 scoured the Roaring River bed below the lake and exposed a lens of organic detritus which has been analyzed for fossil pollen and insect fossils. The fossil site lies at about 2800 m in the ecotone between the upper montane and subalpine forests. Mean July temperature is about 15°C and mean annual temperature averages about 4°C.

The stratigraphic section exposed on the west bank of the Roaring River consists of three units. The lowermost unit is a massive, clast-supported gravel 71 cm thick. This is overlain by the thin organic-rich unit, which was traced over 6 m upstream from the described section. Macrofossils are abundant in this unit and include wood fragments, conifer needles, and conifer cones. The overlying gravel unit is 1.35 m thick with similar textural and compositional characteristics as the lower gravel unit; the contact is planar and abrupt. The two gravel units are interpreted as fluvial gravels deposited during high discharge. Deposition of the organic unit occurred when river discharge was low and channel size occupied by the stream was restricted.

Three radiocarbon dates were obtained from samples of the organic unit (Table III). Two dates (GX-9613 and GX-9612) are from the less than 125 micron organic fraction, whereas GX-9614 is from a sample of wood. The dates are statistically identical and suggest relatively uniform deposition of the

organic unit ca. 2400 years BP.

Insect fossils representing a minimum of 1965 individuals were extracted from approximately 20 kg of organic detritus. Eighty-three insect taxa were identified from three orders, representing 23 families, with 33 specific determinations (Elias, Short, and Clark, submitted: Table 1; Appendix I). There is a great deal of ecological diversity in the fauna, but on the whole the fauna is representative of modern environmental conditions at the site; approximately two-thirds of the species are found in the upper montane and lower subalpine forests of Colorado today.

In the field the 25 cm thick lens was sampled in two intervals, 0-12 cm and 12-25 cm. Pollen analyses were carried out on both subsamples, but the pollen spectra are similar and mean percentage values have been calculated (Elias, Short, and Clark, submitted: Table 2; Appendix I). The Roaring River organic section is dominated by _Pinus_ (48.8%). Other important pollen types include _Picea_, _Salix_ (willow), _Artemisia_ (sage), Chenopodiiaceae (goosefoot family), and Gramineae (grass family). This spectrum is consistent with site loction in the lower subalpine zone. The large NAP (non-arboreal pollen) component plus the importance of willow, grasses and herbs and the large influx of charcoal fragments suggests that open and/or disturbed areas were common immediately around the site, i.e. a flood plain, riparian meadow, or an area disturbed by fire. The first scenario is best supported by the stratigraphic data.

La Poudre Pass Bog

La Poudre Pass is a col on the Continental Divide at the northern end of Rocky Mountain National Park. The pass (altitude = 3103 m) separates the

Colorado River on the southwest from La Poudre Pass Creek, a tributary of the Cache La Poudre River. The site is located in a topographic depression, approximately 300 m downslope from altitudinal treeline. It is presently vegetated with willow shrubs, sedges, and grasses. The trees immediately upslope from the depression are a mixture of subalpine fir and Englemann spruce.

Radiocarbon dates from La Poudre Pass peats have provided valuable evidence in the deglaciation chronology of the northern Front Range (Madole, 1980), revealing that the culmination of the late stade of the Pinedale Glaciation occurred more than 10,000 years ago. Madole (1980) sampled basal peat from two sites, LP-1 (basal date = 9850 BP) and LP-2 (basal date = 8610 BP). A site a few meters away was sampled by Elias for fossil insect study, LP-3 and LP-5, and finally a fourth site, LP-4, was collected for subsequent pollen analyses. Madole noted that field relations between the first two sites gave no cause to anticipate an age difference of 1000 years, and although the older date, 9850 BP, has been assumed for the fossil insect and pollen analyses, the actual date for the subsequent sections may be slightly younger.

Fossil insect fragments representing a minimum of 1858 individuals were extracted from the La Poudre Pass bog; 93 insect taxa were identified, 38 species determinations were among these (Elias, 1983, and submitted). The earliest ecosystem developing after deglaciation of the col appears to have been in wet, open ground. Carex-dominated vegetation probably formed the first stable plant community around the edges of ponds and pools. During the first few centuries of peat accumulation but before the first reliable evidence of spruce migration into the area, summer temperatures were probably quite similar to those found in the modern subalpine forest of Colorado. This

is indicated by the presence of several beetle taxa which today are found in the boreal and montane forest regions but are not directly tied to the trees themselves.

The combination of conifer-attacking bark beetles and spruce macrofossils strongly suggests the presence of spruce trees at or very near the site by about 9500 yr BP; both data sets suggest that subalpine forest was never far from the site from that time to the present (Figure 3). The mixture of alpine tundra and montane forest insects, however, appears to indicate that the altitudinal tree limit was never far from the site during the Holocene.

The sedge-dominated marsh at La Poudre Pass was apparently a very stable plant community for several thousand years in the Holocene. This infers an ample supply of water from snow and glacial meltwater in the col during this interval. Open water was present, at least in small pools, throughout the Holocene. Because of the site's location in a depression, the peat accumulating there must always have been composed of bog-margin vegetation that is deposited between high and low water levels. Because of this telmatic depositional mode, the change in peat composition from sedge to Sphagnum at 25 cm was probably only due to a change in the local water table.

La Poudre Pass Bog was resampled by Elias and Nichols in 1983 for pollen analyses. Two radiocarbon dates have been received for this section (Table III): the basal date of 9850±300 BP from section 3 has been used to date the base of the section reported here. Sedimentation was initially rapid, ca. 50 yr/cm, but this rate subsequently slowed to ca. 100-120 yr/cm in the mid-Holocene. Four pollen zones have been defined on the basis of the pollen stratigraphy (Figure 4).

Zone I, ca. 9800 to 9100? BP, is characterized by maximum Picea and

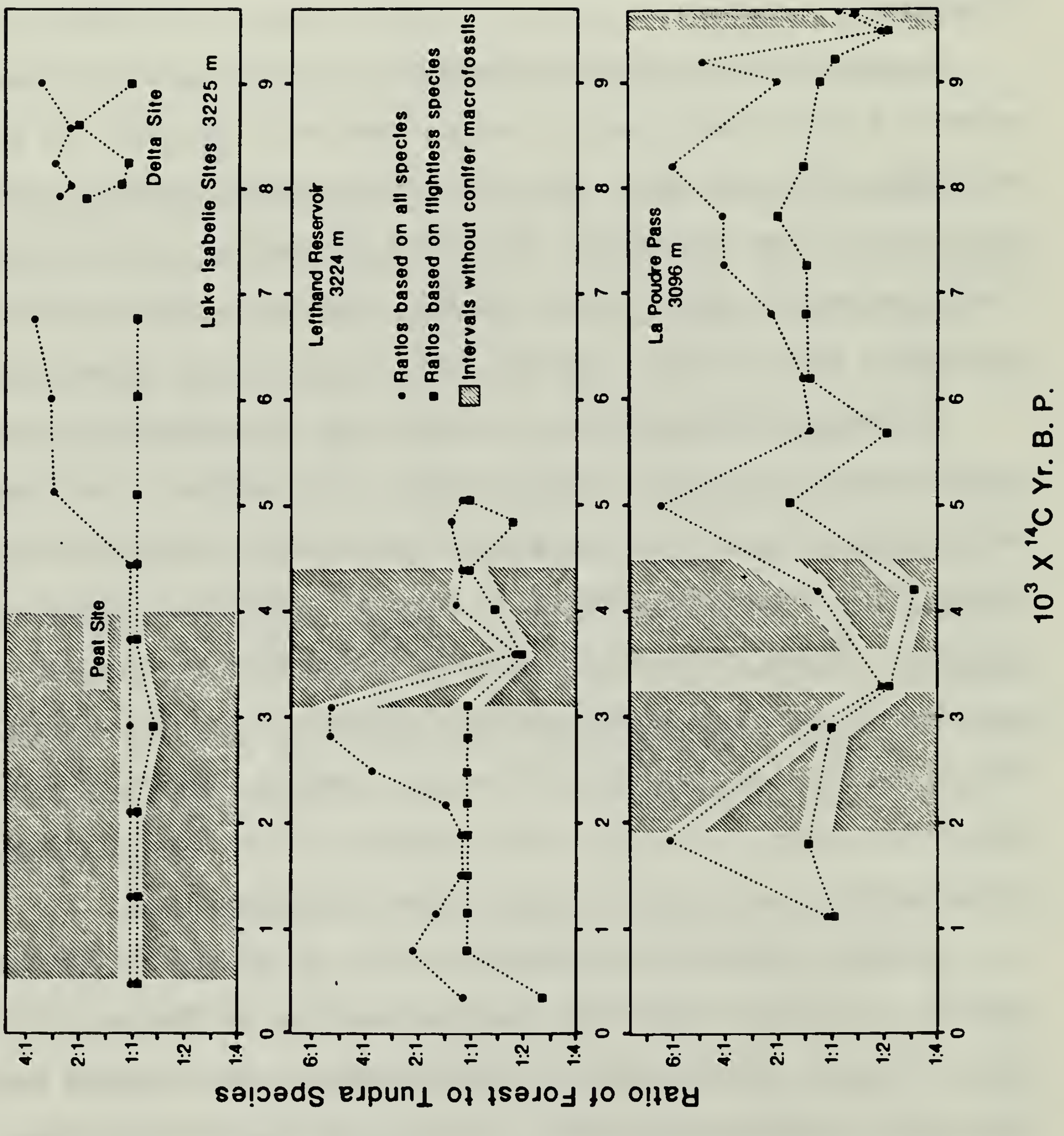

Figure 3. Ratios of forest dwelling to alpine tundra dwelling species from the Lake Isabelle, Lefthand Reservoir, and La Poudre Pass sites.

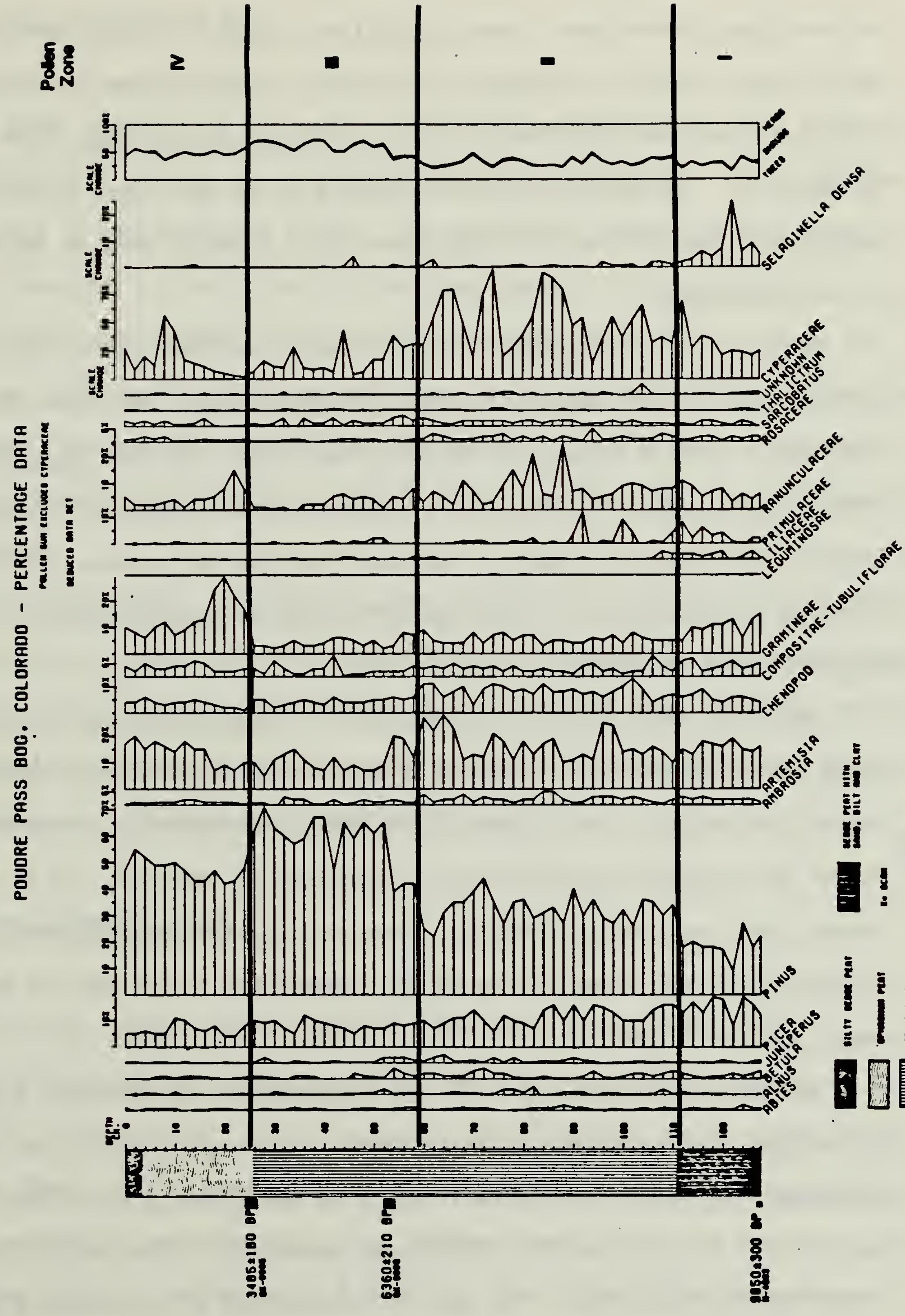

Figure 4. Percentage pollen diagram (reduced taxa set), La Poudre Pass Bog. Pollen sum excludes Cyperaceae.

minimum Pinus percentages, peak Picea/Pinus ratios (.5 to 1), and large NAP percentages, especially Artemisia, Gramineae, Ranunculaceae (buttercup family), Compositae (sunflower family), and Selaginella densa (rock selaginella). Spruce woodland was probably at or very close to the site during this time period, but tundra and shrub elements were an important part of the landscape.

Zone II, ca. 9100?-6800 BP, is defined by moderate but rising Pinus percentages and moderate but decreasing Picea values. Herb taxa are still important, although values are slightly lower here, and the Picea/Pinus ratios remain large, .35-.4. This zone is interpreted as a spruce-fir subalpine forest with some pine; however, the pine treeline was probably still depressed relative to the present. The large NAP component suggests that the vegetation was still open in nature.

Zone III, 6800-3500 BP, is dominated by Pinus percentages and also very large pollen concentration values. Picea percentages decrease only slightly but NAP percentages are minimum. This period represents the time of maximum warmth and presumed maximum extent of treeline at the site. It is uncertain whether the tree species limit of spruce was significantly higher but pine was evidently more important in the forest composition around the col and densities were higher.

The last 3500 years, zone IV, is characterized by decreased Pinus percentages and increased NAP percentages. Although no modern polsters were collected from this site, these values plus the Picea/Pinus ratios (.1 to .2) and the AP (arboreal pollen) percentages appear consistent with collections from similar elevations. This zone is interpreted as representing modern day conditions at La Poudre Pass.

Lefhand Reservoir Bog

A sedge bog lies at the upper end of Lefthand Reservoir, 6.25 km east of the Continental Divide, at an altitude of 3224 m (Figure 2). The catchment basin area is approximately 5 km^2. The temperature regime at this site is nearly identical to that noted for the Lake Isabelle sites (Kiladis, unpublished report, 1980). The bog is bounded by subalpine forest on the north and west, by forest-tundra scrub on the south, and by the reservoir on the east. The 1-m peat section was sampled and a single basal radiocarbon date of 7760±160 BP obtained in 1978. Insect analyses have been completed for this site.

A minimum of 591 individual insects representing 49 taxa were recovered, all but five of which were also found in the Lake Isabelle delta assemblages. The data indicate that spruce and fir were present at this site from the date of deposition (Figure 3). There are also riparian and lake species indicative of montane and subalpine environments (Appendix I).

Lake Isabelle Sites

The Lake Isabelle basin (3310 m) lies about 1.5 km east of the Continental Divide and is fed by meltwater from the Isabelle Glacier in the South St. Vrain Valley. It is located in the subalpine forest-alpine tundra ecotone (Marr, 1967); outlier islands of krummholz trees (*Picea engelmannii*, *Abies lasiocarpa*, and *Pinus flexilis* [limber pine]) extend to the lake. The catchment basin is approximtely 5.8 km^2 in area. Mean July temperature at the study site is about 10.5°C (Kiladis, unpublished report, 1980). Based on extrapolation from 30 years of temperature data from sites on Niwot Ridge

Niwot Ridge just to the south, mean annual temperature is about 0°C (Losleben, 1983). A short section of sedge peat is located along the southwestern margin of the lake; an organic-rich deltaic deposit was discovered at the mouth of the creek during September 1981, when the lake water level was exceptionally low.

Lake Isabelle, Delta Site

The radiocarbon dates (Table III) indicate that the upper portion of the section was deposited very rapidly, perhaps in a single event. For the purpose of the fossil study, the upper 0.40 m of the section was treated as a bulk sample with an averaged age of 7900 yr BP; thus the record from the delta sites is believed to represent the period from 9000 to 7900 yr BP.

This section has been analyzed for fossil insects and has produced the greatest number of fossil insect specimens of any of the sites discussed here. A minimum of 3050 individual fossil insects are represented, and excluding Trichoptera (caddis flies), includes 136 insect taxa from 25 beetle families in addition to five ant taxa and parasitic Hymenoptera (Appendix II): 66 specific identifications were made.

The fossil assemblages indicate the nearby presence of trees for this period. The ratios of forest-to-tundra species (Figure 3) based on the number of identified species from the delta assemblages would suggest that tree limit was higher than present during this interval, whereas the more conservative set of ratios (which excludes bark beetles and other flying taxa) indicates at least one major treeline oscillation in the same period. The most reliable estimate of the forest-tundra species ratios undoubtedly lies between the two

sets of ratios shown.

Lake Isabelle Bog

Three radiocarbon dates (Table III) have been received for this site. They indicate an initially slow rate of sedimentation, 200 yr/cm, in the basal sandy sedge peat to ca. 3300 BP. Subsequently, the sedimentation rate increased to between 40 and 90 yr/cm. Both pollen analyses and insect studies have been conducted at this site.

Relatively high tree limits from 7000 to about 4500 BP are suggested by the "all species" ratios in the insect data (Figure 3). Following this, a remarkably constant forest-to-tundra insect species ratio is found in all subsequent assemblages. This, combined with a lack of conifer macrofossils in most of this interval, suggests that the sedge meadow above Lake Isabelle became very stable or perhaps extended during the past 4500 yr BP to the exclusion of the coniferous forest. It is unknown whether this vegetational stability was due to climtic, edaphic, or biological factors and this seeming complacency of the fossil insect record allows litle paleoenvironmental interpretation. It is, however, perhaps suggestive of climatic conditions cooler than the 7000 to 4500 yr BP period, and either cooler than or similar to modern conditions.

Four pollen zones have been defined for this site on the basis of the pollen stratigraphy (Figure 5). The basal zone I, 7900 to ca. 3900 or 4000 BP, is characterized by maximum Picea percentages, low Pinus values, maximum Picea/Pinus ratios (.3-.45), and large NAP percentages. Pollen concentration values (i.e., numbers of grains per gram dry weight) are low. This spectrum

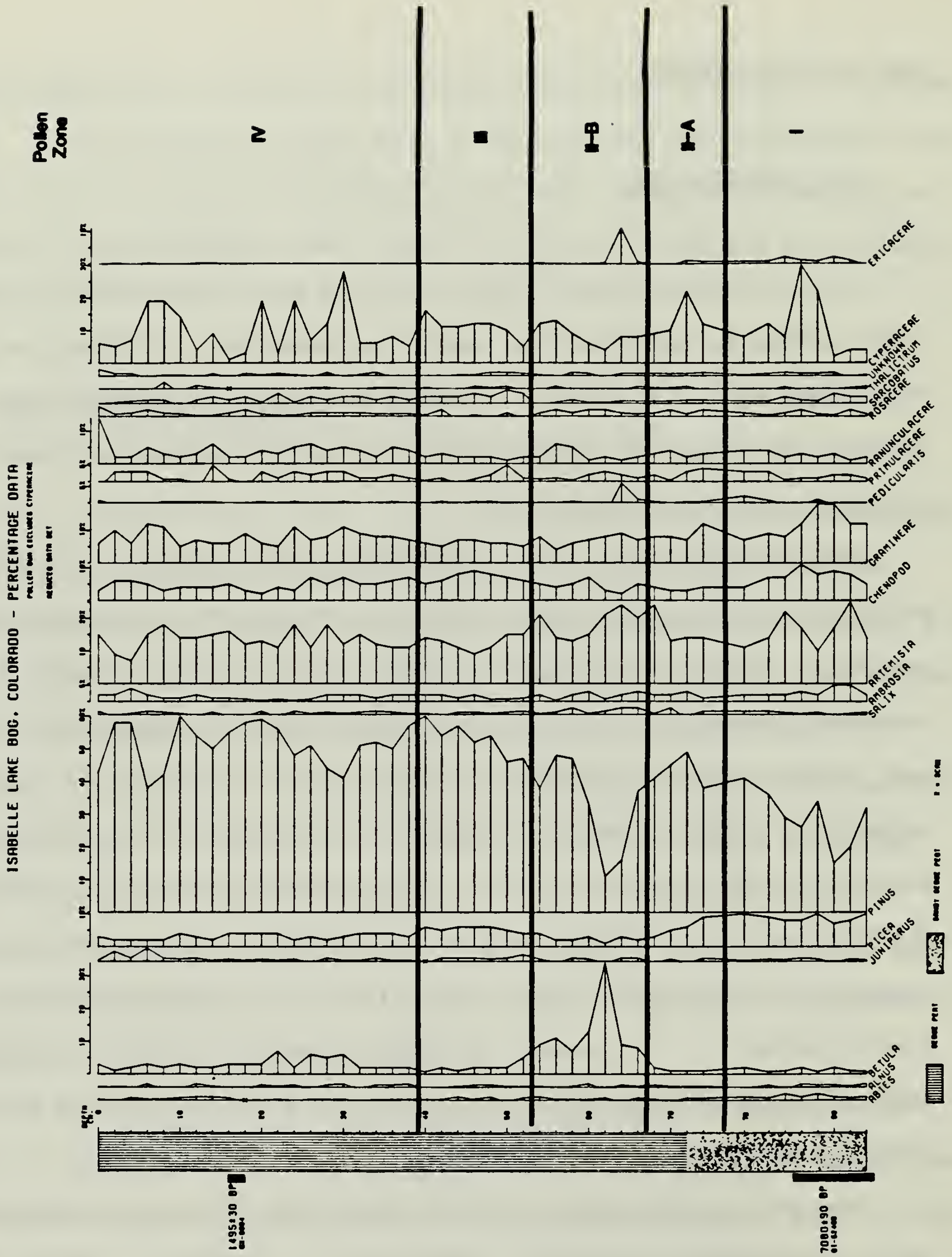

Figure 5. Percentage pollen diagram (reduced taxa set), Lake Isabelle Bog. Pollen sum excludes Cyperaceae.

suggests an open spruce-fir woodland with a large shrub tundra component.

Zone II is subdivided by an important local event, the Birch Period. Initially, from 3900 to approximately 3100 BP, this zone is characterized by rising Pinus percentages, moderate Picea values, and moderate NAP values; pollen concentrations are rising here. This pollen spectrum is indicative of a rising pine limit and possibly increased conifer density at the site. Zone IIB, 3100 to 2650 BP, is designated the Birch Period because it is dominated by moderate to large Betula (birch) percentages and concentration values. Other shrubs (Ericaceae [heath family], Salix) and herb pollen types are also important and AP percentages are very low. This spectrum is interpreted as a local event, representing the drying out of the bog surface and the invasion by shrubs.

Zone III, 2650 - 2250 BP, marks the recovery of arboreal pollen types due to rising Pinus percentages and moderate Picea values. This period is interpreted as the maximum extent of tree growth at this site with increased representation of both pine and spruce individuals.

In Zone IV, 2250 BP to the present, Pinus percentages dominated the pollen spectrum. Herb pollen percentages are low to moderate, but several NAP curves record increased values in approximately the last 700 years. A second minor birch episode is recorded from approximately 1900 to 1600 BP. This zone represents a decrease in tree limit at this site; the very large Pinus percentages are indicative of the over-representation of this productive genus. This is supported by the low Picea/Pinus ratios (mean = .06), which are similar to those recorded in modern moss polsters from the site.

Mount Ida Ridge Pond

This site is an isolated pond, less than 0.1 ha in size, located about 1 km east of the Continental Divide in Rocky Mountain National Park on a broad plateau (Figure 1). The pond lies below Mount Ida Ridge, at an altitude of 3520 m, in the alpine tundra. The catchment basin is less than 1 km^2. Mean July temperature at the study site is about 9°C and mean annual temperature about -2°C. The pond appears to be spring-fed, and is held back by a rock bar. Sedge peat has accumulated at the margins of the pond. A sediment core was collected during September, 1982. Three radiocarbon dates have been received for this section (Table III) and suggest that the basal half of the section dates to a single time period (i.e., between 8400 and 9000 BP). The upper portion of the peat has a confused chronology, limiting paleoecological interpretations.

A maximum number of 267 individuals, representing 40 insect and crustacean taxa, including 14 specific determinations, were recovered from the core; each 0.1 m interval sampled for insect fossils contained less than 1 L. of sediment, which is less than a quarter of the volume of the samples from the Lake Isabelle sites. Therefore, the small sample sizes and degree of uncertainty concerning the radiocarbon dates make the paleoenvironmental interpretations more tentative than the other sites.

The two sets of forest-tundra insect species ratios (Figure 6) are very close together, due to the small number of flying beetles in the assemblages. Between 9000 and 8300 BP, the ratios suggest that conditions were similar to today, with tree limit downslope from the site. An apparent climatic optimum was reached, probably within a few centuries after 8300 BP, and tree line may

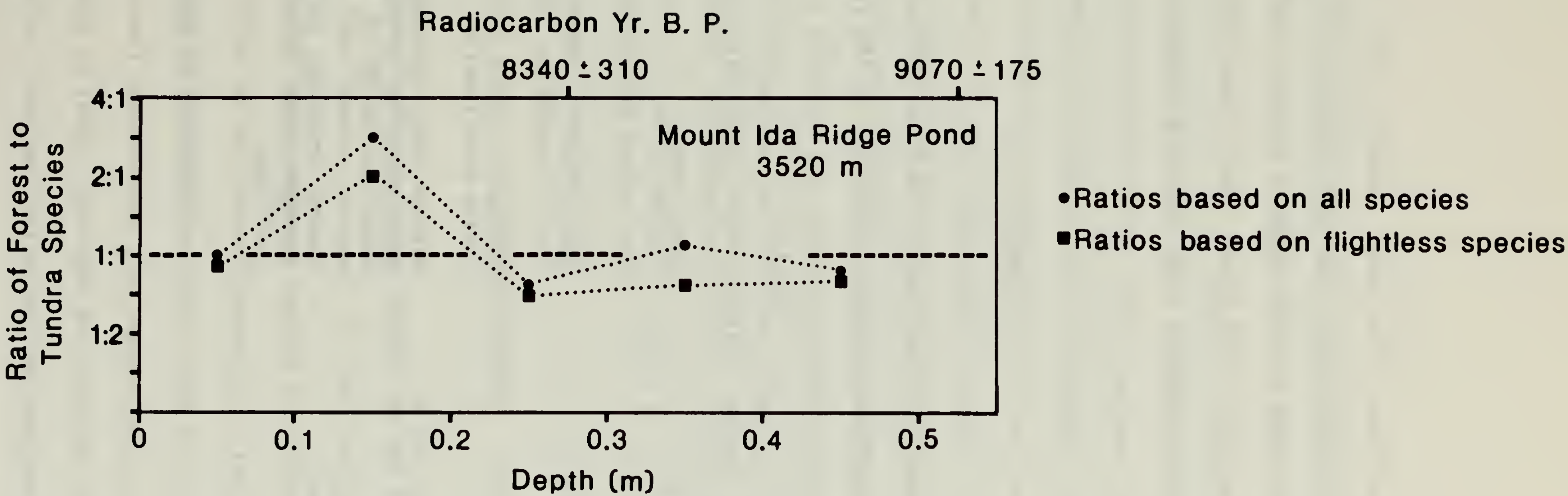

Figure 6. Ratios of forest dwelling to alpine tundra dwelling beetles species from the Mount Ida Ridge Pond site.

have advanced to the altitude of the pond. However, there is no conifer macrofossil evidence to suggest that conifers colonized the immediate vicinity. Modern tree limit in Rocky Mountain National Park is approximately 50 m downslope from the pond, but numerous dead, standing tree stumps (see above) have been found above modern tree line at altitudes up to that of the pond site.

SUMMARY

The regional history of vegetational change as interpreted in the pollen record from the Colorado Front Range is summarized in the following table:

TABLE IV

VEGETATIONAL SUMMARY, COLORADO FRONT RANGE POLLEN CHRONOLOGY

12,000 - 10,500 BP	Shrub tundra
10,500 - 9,500 BP	Open spruce forest-shrub tundra
9,500 - 9,000 BP	Open spruce-fir forest Treeline advancing upslope
9,000 - 6,500 BP	Spruce-fir forest similar to present; rising pine treeline
6,500 - 4,000/3,500 BP	Maximum pine representation in upper subalpine forest; maximum warmth and extent of treeline
4,000 - present	Lowered treeline; increased herb representation; cooler climatic conditions

This scheme is not in phase with that presented by Maher in his Redrock Lake study (1972), but does compare well with studies from southern Colorado (Andrews *et al*., 1975; Petersen and Mehringer, 1976) as assessed by Nichols (1982). Maher utilized detailed statistical analyses, including the use of

spruce/pine ratios, in his study, and these are now being applied to these sites. Preliminary results suggest that the above reconstruction will be supported. However, the fossil insect data indicate that climatic deterioration was initiated by 4500 BP in these sites. The timing is 500 - 1000 years earlier than the pollen record indicates and requires additional research to examine the causes of this discrepancy. Similarly, a brief amelioration of climate (and advance of treeline) from 3500 BP to perhaps 1000 BP is also picked up in the insect studies but not in the pollen spectra.

These data, along with the dates on sub-fossil tree stumps in the lower alpine ranging from 200 - 1700 BP, suggest that the concept of ecosystem metastability is valid for the alpine/subalpine ecotone, and that some elements of that ecotone are relicts from warmer climates and thus are not fully in equilibrium with modern econditions. Increasingly the upper treeline regions seem to be a fragile ecotone, subject to irreversible damage.

ACKNOWLEDGEMENTS

We would like to acknowledge the support of the CULTER program (NSF # DEB80-12095) to this research program. R. Kihl, INSTAAR Sedimentology Laboratory, prepared fossil sediment samples for radiocarbon dating. Dr. R. Stuckenrath, Smithsonian Radiocarbon Laboratory, kindly provided several radiocarbon dates for the project.

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APPENDIX I

Late Holocene Paleoecology of the
Roaring River Site, Rocky Mountain
National Park, Colorado

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ABSTRACT

The catastrophic dam failure at Lawn Lake, Rocky Mountain National Park, scoured the Roaring River bed below the lake and exposed a lens of organic detritus which has been analyzed for fossil pollen and insect fossils. The site is located at 2800 m in the ecotone between the upper montane forest and the lower subalpine spruce-fir forest. The analyses suggest that the local environmental conditions 2400 years ago were similar to the present and that coniferous forest was in close proximity to the site. However, the nearby presence of open and/or disturbed areas is also strongly supported by both the pollen and insect data.

INTRODUCTION

On July 15, 1982, an earthen dam failed at Lawn Lake, Rocky Mountain National Park, releasing 674 acre feet of water in a catastrophic flood down the Roaring River Valley. Peak discharge of the flood has been estimated at 18,000 cubic feet per second. Geomorphic effects of the flood were extreme in the Roaring River Valley, widening the channel by up to several meters, and scouring the bottom to depths of 1.5 to 15 m (R. D. Jarrett, pers. comm., 1984). At a point along the Roaring River, approximately six km downstream from Lawn Lake, the flood waters scoured a section of the west bank, exposing a lens of organic detritus approximately 0.7 m above the post-flood stream edge (Fig. 1). This organic lens has been analyzed for fossil pollen and insect fossils.

Lawn Lake occupies a moraine-dammed depression in the southeastern portion of the Mummy Range, at an elevation of about 3350 m above sea level. The Roaring River originates in Crystal Lake, a tarn lake about 1.6 km upstream from Lawn Lake. It feeds Lawn Lake, and then descends across a broad, till covered valley, along slopes averaging 10%. The bedrock in this region consists of Precambrian gneisses and schists more than 1.7 billion years old (Peterman _et al_., 1967).

The fossil site lies at about 2800 m above sea level, in the ecotone between the upper montane and subalpine forests (Marr, 1967). Annual precipitation at the site averages approximately 700 mm per year. Mean July temperatures at this elevation are about 15°C, and mean annual temperatures about 4°C. The local forest vegetation along the river banks at the site is a mixture of tree species from the two adjacent ecosystems, namely, _Pinus_

contorta var. *latifolia*, *Abies lasiocarpa*, *Picea engelmannii*, *Pinus ponderosa*, *Populus tremuloides*, and *Pseudotsuga menziesii*.

METHODS

The organic lens was sampled by the authors in June, 1983. The 0.25 m thick lens was sampled in two intervals, 0 - 0.1 m and 0.12 - 0.25 m. After cleaning the face, three samples of approximately 3.75 ℓ each were taken from the two sampling intervals, and transported in plastic bags to the Institute of Arctic and Alpine Research (INSTAAR) for study. Two additional samples of the same volume were taken from each of the two sampling intervals by Elias two weeks later to provide additional material for fossil insect study. Small subsamples (136 and 166 g, respectively) were submitted from the two intervals for radiocarbon assay, as well as a piece of wood from the uper 0.12 m. Additional small subsamples were taken from each level for pollen analysis. The remainder of the samples were washed in a 300 μm mesh sieve, and then processed by the kerosine flotation method (cf. Coope, 1968) for concentration and extraction of insect fossils.

The insect fossils were sorted in alcohol under low power stereo binocular microscope. Identifiable fragments were either mounted with gum tragacanth (a water soluble glue) onto modified micropaleontology cards (more robust specimens), or stored in vials of alcohol (fragile specimens and numerous duplicates). Caddisfly (Trichoptera) larval fragments were mounted in Polyvinyl lactophenol medium on glass slides. A list of the fossil insect fauna and associated habitat and ecological requirements is shown in Table 1. The standard procedure of establishing the minimum

number of individuals of each taxon per studied interval has not been performed on this set of data, because close agreement of radiocarbon ages from the two intervals indicates that the entire lens should be treated as of one age (see below).

Standard preparation techniques, modified from Faegri and Iversen (1975), were used to prepare sediment samples for pollen analysis. Counts of 200 pollen grains, excluding Cyperaceae, were carried out for each interval and 25 pollen types were identified. Percentage data for major pollen types are shown in Table 2. Identifications were made with reference to the INSTAAR pollen reference collection. Pollen concentration values ranged from 100,000 to 200,000 grains/gm weight; these are slightly lower than pollen concentration values from several unpublished peat sections in the region (Short, unpublished data).

LITHOSTRATIGRAPHY

Section Description: The stratigraphic section exposed on the west bank of Roaring River consists of three units (Figure 2). The lowermost unit is a massive, clast-supported gravel 71 cm thick with slight imbrication of some clasts (facies Gm; Miall, 1977). Locally derived gneissic gravel is subrounded to rounded. Pebbles are most common, but several boulders up to 70 cm in size were exposed. Matrix sediment is coarse sand.

An organic-rich unit 25 cm thick overlies the gravel (Figure 2). This unit is draped over boulders where in contact with the gravel. The organic unit was traced over 6 m upstream from the described section, where it thins and wedges out. The organic unit is a very poorly sorted (Ø = 4.32),

strongly fine skewed (Sk = 0.9), black clayey sand (Shepard, 1954; Folk and Ward, 1957). Small pebbles are scattered throughout the unit, and there are several discontinuous laminae of sand 1-2 mm thick. No other indication of bedding was observed.

The unit contains 10.6% organic matter in the < 2000 μm fraction. Macrofossils are abundant, however, and we estimate that total organic matter constitutes at least 50% of the sediment. Macrofossils include wood fragments, conifer needles, and conifer cones. These have been slightly flattened, suggesting post-depositional compaction.

The contact between the organic unit and the overlying gravel unit is planar and abrupt. This gravel unit is a massive framework gravel 1.35 m thick with similar textural and compositional characteristics as the lower gravel unit (i.e. facies Gm).

Depositional Environments: The two gravel units are interpreted as fluvial gravels deposited during high discharge. Miall (1978) and Rust (1978) interpret fluvial lithofacies such as these as characteristic of deposition by longitudinal bars in proximal fluvial environments.

Deposition of the organic unit occurred when river discharge was low and channel size occupied by the stream was restricted. Organic and mineralogic sediment accumulated in a depression (abandoned stream channel) on the valley floor. Deposition was isolated from stream processes except for incursions of overbank sedimentation. High percentages of fine sand and silt were probably derived from eolian deflation of adjacent exposed fluvial sediments and overbank flooding. Scattered pebbles may represent sediment input from slopes adjacent to the depositional depression.

CHRONOLOGY

Three radiocarbon dates were obtained from samples of the organic unit (Figure 2). Two dates (GX-9613 and GX-9612) are from the < 125 μm organic fraction, whereas GX-9614 is from a sample of wood macrofossils. The dates are statistically identical and suggest relatively uniform deposition of the organic unit ca. 2400 yrs B.P.

FOSSIL INSECT FAUNA

Organic detritus collected from the Roaring River site was extremely rich in insect fossils, in addition to abundant seeds, conifer needles, wood and cones. Insect fossils representing a minimum of 1975 individuals were extracted from approximately 20 kg of organic detritus. Eighty-three insect taxa were identified from three insect orders, representing 23 families (Table 1).

Thirty-three specific determinations have been made (40%). Faunal assemblages have been treated as one unit, as described in the methods section (above). There is a great deal of ecological diversity in the insect fauna. Although terrestrial taxa predominate in the assemblages, a substantial aquatic element was found in each sample, including not only aquatic beetles, but also caddisfly larvae. Among the terrestrial fauna, beetles are numerically dominant, but significant numbers of ant fossils were also found.

Discussion of Selected Taxa

Ground beetles (Carabidae) constitute a large and ecologically important part of the Roaring River fossil insect fauna. A variety of habitats in the vicinity of the fossil site may be reconstructed on the basis of the modern ecological records for specifically identified carabids. Carabus taedatus agassi (Fig. 3, A) is a xerophilous species, preferring open ground of gravelly soil with thin, low vegetation. This species is also occasionally found in open coniferous forests in North America (Lindroth, 1961). Notiophilus directus (Fig. 3, B) also lives mostly on open ground today, occurring mainly in riparian habitats. The principal habitat of Bembidion incertum (Fig. 3, C) is at snowfield margins, mainly above tree limit in western mountain ranges of North America. Agonum bembidioides is known to inhabit burnt forest ground. The peculiar black mottled appearance of this species (Fig. 3, D) blends well with a background of charcoal litter (Lindroth, 1966). The latter three of the above species are restricted to the western parts of North America today, but Carabus taedatus agassii has isolated populations in the Great Whale River region and at Blanc-Salbon (near the southeastern border with Labrador) in Quebec (Larochelle, 1975).

Calathus advena (Fig. 3, E) is a carabid beetle found primarily among leaves and debris on shaded forest floors. Its modern distribution is disjunct, with a gap in the central plains region of North America (Lindroth, 1966). The distribution of Selenophorus gagatinus lies today in eastern North America, at least as far west as Indiana, but as yet unrecorded from Colorado. This beetle (Fig. 3, G) has been found on "high, dry hills" within its modern range (Lindroth, 1968). The most cold-adapted

species of ground beetle from the Roaring River fauna is Trichocellus mannerheimi (Fig. 3, H), which today has an arctic and alpine distribution in North America, although some specimens have been collected from the upper forest regions (Lindroth, 1968). T. mannerheimi apparently prefers open ground situations with dry, sandy soils and scarce vegetation. Stenelophus conjunctus (Fig. 3, I) is also found on open ground, but is a xerophilous species found in dry country across North America. This beetle is frequently taken from sand pits (Lindroth, 1968).

A number of rove beetle taxa (Staphylinidae) in the subfamily Omalinae are represented in the Roaring River assemblages. Among these are the species Eucnecosum brunnescens, Eucnecosum tenue, Olophrum consimile, Olophrum rotundicolle and Acidota quadrata. These species have broadly overlapping habitats at high altitudes in the Rocky Mountains, namely, moist localities, often near streams or ponds. They are found in leaf litter, mosses and other wet vegetation, predominantly in the upper forest and the alpine tundra (Campbell, 1982, 1983, 1984). Other staphylinid beetles of interest from the Roaring River fauna include Tachinus elongatus and Tachinus frigidus. T. elongatus is a holarctic, boreo-montane species, taken at 3660 m asl in Rocky Mountain National Park (in alpine tundra). This beetle is often found in damp places, near snow patches or small streams, especially in wet mosses or leaf litter. T. frigidus is likewise a boreo-montane species, but is found mostly under animal dung (Campbell, 1973).

Several of the Roaring River beetle taxa are known to attack species of Pinus. The bostrichid, Stephanopachys sobrinus, has been found on pines throughout the western mountains of North America (Fisher, 1950).

Stephanopachys larvae bore into bark, wood or cones of conifers (White, 1983). The weevil (Curculionidae), Magdalis hispoides, is widely distributed in North America. It bores into the bark of several species of pines (Fall, 1913; Blatchley and Leng, 1916). Dendroctonus brevicomis is a bark beetle (Scolytidae) found mostly on Pinus ponderosa and P. coulteri in western North American mountains. In historical times, epidemic outbreaks of this species have occurred in which other tree species have also been attached (Wood, 1982).

Other scolytid species from the Roaring River fossil list are known to attack Picea, either primarily or exclusively. Scolytus piceae is a boreo-montane, transamerican species that is found mostly on shaded-out branches of spruce. Dendroctonus rufipennis has a similar distribution pattern, and attacks windfallen, dying green spruce trees. Epidemics of this species have also occurred recently, in which healthy spruces, as well as other tree genera have been attacked (Wood, 1982). Recently fallen, broken or cut spruces are frequently attacked by Polygraphus rufipennis, although this widely distributed species is also found on firs and pines. Finally, the scolytid, Dryocoetes affaber, is known to bore into the lower bole, stumps and limbs of moribund or dead spruces across the boreo-montane regions of North America.

The ants, Camponotus herculeanus and Formica rufa marcida, are also associated with coniferous forests in North America. C. herculeanus, a carpenter ant, builds its nest from conifer wood across Holarctic regions. F. rufa marcida occurs today in western North American mountains from Alaska to Arizona. This subspecies has been found at elevations up to altitudinal tree limit, and builds its nest in soil, mostly under rocks (Francoeur,

1973).

Among the caddisfly genera identified from the Roaring River site, several are indicative of cold, fast-moving mountain streams. These include the Hydropsychid, *Arctopsyche*, the Limnephilids, *Clistoronia* and *Dicosmoecus*, and the Rhyacophilid, *Himalopsyche*. *Arctopsyche* larvae live in streams where retreats are located in strong currents. These net spinning caddisflies catch other invertebrates moving in the water. *Clistoronia* caddis larvae live in western mountains of North America, at high elevations. *Dicosmoecus* larvae are also restricted to western North American streams, and fix their larval cases to the underside of rocks. *Himalopsyche* is another genus restricted to the mountains of western North America (Wiggins, 1977). Additional taxonomic research on the fossil caddis larvae from this site may reveal more specific ecological information.

Summary of Ecological Groupings in the Fauna

The habitat and ecological requirements of 49 of the Roaring River insect taxa are shown in Table 1. Two-thirds of these taxa live in terrestrial habitats, one-third live in aquatic habitats, predominantly in streams. Of the terrestrial group, 65% are associated with coniferous forest environments, and 26% are found in open ground situations. Thirteen percent of the terrestrial taxa are xerophilous, and 34% are associated with wet habitats.

POLLEN DATA

The two pollen spectra are similar and therefore a mean value was calculated. The Roaring River organic section is dominated by *Pinus* (pine)

percentages (48.8%). Other important pollen types include Picea (spruce) (5.5%), Salix (willow) (11%), Artemisia (sage) (6.8%), Chenopodiaceae (goosefoot family) (5%), and Gramineae (grass family) (7%). The values for Abies cf. lasiocarpa (subalpine fir), the ecosystem co-dominant, are low, but this taxa does not contribute significantly to the pollen rain in the subalpine.

Discussion of Pollen Spectrum

The AP% value is calculated as the sum of Abies, Picea, and Pinus in this study. It is included here because it is a commonly used estimate of the importance of tree versus non-arboreal pollen (NAP) in an area and may be compared to other studies. Values for the Picea/Pinus ratio are also included in Table 2. This ratio is based on the exponential model of pollen production and many workers have postulated the use of ratios of different pollen taxa in describing the pollen rain of different vegetation zones. This approach has been used successfully in a number of western pollen studies (Maher, 1961, 1963, 1972; Baker, 1979; Andrews et al., 1975; Petersen and Mehringer, 1976). Maher (1961) introduced a number of ratios, but was only able to use one, the Picea/Pinus ratio, in his later Front Range work (1972). Maher found that by plotting the Picea/Pinus ratio on semi-logarithmic paper a diffuse trend could be found (1972: Fig. 6). The ratio attains its maximum values in the subalpine zone (ca. 2470 m to timberline, eastern slope). In adjacent zones, i.e., upper montane and tundra, Pinus values increase and the ratio decreases; the problem of a single ratio being representative of two elevations, one below timberline and the other above timerline, is discussed by Maher (1972). The value

reported in this study (.12) is therefore predicted for two elevations in Maher's Front Range study, ca. 2900 m and 3450 m.

Charcoal fragments were frequently encountered on the slides from the Roaring River organic section. Charcoal fragments are commonly recovered in lake and peat sediments from the Front Range, (Short, unpublished data), but no hard data are available for comparison. However, charcoal fragments appear more numerous in this site.

INTERPRETATION

Richmond (1960) mapped late Holocene glacial deposits and protalus rampart in cirques at the head of Roaring River. He interpreted these deposits to be Temple Lake (= Early Neoglacial; Dowdeswell, 1982) and historic (= Gannett Peak; Dowdeswell, 1982) in age. Deposition of the organic unit ca. 2400 yrs BP thus occurred between Early Neoglacial (ca. 3000-5000 years old; Benedict, 1973) and Gannett Peak (ca. 300-100 yrs old; Benedict, 1973) expansions of cirque glaciers upvalley. Absolute dating of gravel units above and below the organic unit is not possible. Neoglacial expansion of cirque glaciers may account for increased discharge suggested by the gravel units. However, episodic flooding is an equally viable process for gravel deposition. Until the gravel units can be dated or traced upstream to glacial deposits, their environmental significance (i.e. glacial or flood) remains unknown.

Pollen data support the interpretation that the organic unit was uniformly deposited due to the similarity of the two pollen spectra. The pollen spectrum is consistent with site location in the lower subalpine

zone; this is based on the pollen percentages and on the Picea/Pinus ratio of 0.12 which is correlated with an elevation similar to the site.

Moss and lichen polsters have been collected from an altitudinal transect in Rocky Mountain National Park but have not yet been analyzed. In this study, pollen data have been compared to the modern record from a study of the eastern and western slopes of the central Rocky Mountains, Colorado (Millington, 1977). The Roaring River site compares most favorably with Millington's western slope subalpine forest polster samples which are generally from more open sites (1977:49). The large NAP component from the Roaring River site, the importance of willow, grasses, and herbs and the large influx of charcoal fragments suggests that open and/or disturbed areas were common immediately around the site, i.e., a flood plain, riparian meadow site, or an area disturbed by fire.

Insect faunal assemblages from this site appear to represent a mixture of locally derived and exotic specimens, based on their modern distribution and ecological requirements. Approximately two-thirds of the species found in the assemblages are found in the upper montane and lower subalpine forests of Colorado today, including many of the ground beetles, rove beetles, weevils and bark beetles. A smaller component (ca. 25%) is derived from the subalpine forest-alpine tundra ecotone and alpine tundra zones. Most of these taxa are flightless, and were therefore probably carried downstream by the paleo-Roaring River. A small number of species were found which live today at elevations well below the site. These are all full-winged beetles, and were probably carried upslope to the site by winds.

On the whole, the fossil insect fauna is representative of modern environmental conditions at the site, as a collection of dead insects in the

stream flotsam from this elevation today would undoubtedly include a mixture of locally derived and exotic specimens. As in the pollen interpretations, the fossil insects suggest the nearby presence of open ground, either of meadow vegetation or of a broad riparian nature. Certainly the coniferous forest was in close proximity to the site at 2400 yr. B.P., and it included such genera as Pinus, Picea, Abies and Pseudotsuga, as evidenced by the bark beetle fossil record. Ecological requirements of aquatic insects represented in the Roaring River fossil record would indicate that environmental conditions at the Roaring River site ca. 2400 yrs B.P. were similar to those found today.

ACKNOWLEDGEMENTS

We would like to thank Scott Lehman for bringing the site to the authors' attention. R. Kihl, INSTAAR Sedimentology Laboratory, prepared the samples for radiocarbon dating and performed the sedimentological analyses presented here. Drs. J. M. Campbell and D. E. Bright, Biosystemtics Research Institute, Ottawa, Ontario, identified fossil beetle specimens. Dr. A. Francoeur, University of Quebec, Chicoutimi, identified fossil ant specimens and Bridget Wilkinson, London, England, identified caddisfly larval fossils. Mr. R. D. Jarrett, U. S. Geological Survey, Denver, allowed us acess to unpublished data on the Lawn Lake flood. Dr. D. R. Stephens, Rocky Mountain National Park cooperated in allowing the sampling of fossil materials and modern specimens in the park, and funding for this research was provided by the National Park Service, under a grant, #CX-1200-2-B048, for paleoecological studies in Rocky Mountain National

Park. Additional support for this research was provided by a National Science Foundation, Long-Term Ecological Research Grant, BSR-8012095.

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Figure Captions

1. Map of the Roaring River study site, Rocky Mountain National Park.

2. Stratigraphy and dating chronology of the Roaring River site.

3. Photomicrographs of Roaring River insect fossil specimens. A - Apical half, left elytron of *Carabus taedatus agassii*, B - Left elytron of *Notiophilus directus*, C - Left elytron of *Bembidion incertum*, D - Left elytron of *Agonum bembidioides*, E - Pronotum of *Calathus advena*, F - Left elytron of *C. advena*, G - Left elytron of *Selenophorus gagatinus*, H - Left elytron of *Trichocellus mannerheimi*, I - Pronotum of *Stenelophus conjunctus*.

Table Titles

TABLE 1. Taxonomic List of Insect Fossils from the Roaring River Site

TABLE 2. Pollen Percentage Data (selected pollen types), Roaring River Site

Taxon	Habitat and Ecological Requirements
COLEOPTERA	
Carabidae	
Carabus taedatus agassii LeC.	SA, T, x
Notiophilus directus Csy.	SA, o
Bembidion incertum Mots.	T, SA, sn
Bembidion striola LeC.	SA, r
Bembidion cf. _transversale_ Dej.	M, r
Trechus sp.	
Pterostichus sp.	
Calathus advena LeC.	M, SA, cf
Agonum bembidioides Kby.	M, SA, cf, ch
Agonum sp.	
Amara cf. _apricaria_ Payk.	M, SA, o, mdw.
Trichocellus mannerheimi Sahlb.	T, SA, o
Selenophorus gagatinus Dej.	M
Discoderus sp.	
Stenelophus conjunctus Say	x, o
Metabletus americanus Dej.	x, o
Dytiscidae	
Genus indet.	A

Taxon	Habitat and Ecological Requirements
Hydrophilidae	
Helophorus sp.	A
Genus indet.	
Staphylinidae	
Micropeplus laticollis Mäkl.	M, SA, cf
Oxytelus sp.	
Eucnecosum brunnescens Sahlb.	T, SA, w
Eucnecosum tenue (LeC.)	T, SA, w
Eucnecosum spp.	
Unamis sp.	
Phlaeopterus sp.	
Olophrum consimile Sahlb.	T, SA, w
Olophrum rotundicolle Sahlb.	T, SA, w
Olohprum spp.	
Acidota quadrata (Zett.)	T, SA, w
Microedus sp.	
Orobanus sp.	
Geodromicus sp.	
Xantholinus sp.	
Philonthus sp.	
Quedius sp.	
Lordithon spp.	

Taxon	Habitat and Ecological Requirements
Bryoporus sp.	
Mycetoporus sp.	
Tachinus elongatus Gyll.	SA, T, sn, W
Tachinus frigidus Er.	SA, T, d, w
Tachinus sp.	
cf. *Deinopsis* sp.	
Histeridae	
Genus indet.	
Scarabaeidae	
Aegialia lacustris Le C.	T, SA, o
Aphodius sp.	d
Byrrhidae	
Simplocaria sp.	o
Elmidae	
Genus indet.	A
Elateridae	

Taxon	Habitat and Ecological Requirements
Genus indet.	
Cantharidae	
<u>Podabrus</u> sp.	
Anobiidae	
Genus indet.	
Bostrichidae	
<u>Stephanopachys</u> <u>sobrinus</u> Csy.	M, SA, cf (<u>Pinus</u> spp.)
Nitidulidae	
cf. <u>Epurea</u> sp.	
Cucujidae	
<u>Laemophloeus</u> sp.	
Mycetophagidae	

Taxon	Habitat and Ecological Requirements
Genus indet.	
Cerambycidae	
Genus indet.	
Chrysomelidae	
Oedionychis sp.	
Altica spp.	
Curculionidae	
Apion sp.	
Magdalis hispoides Le C.	M, SA, cf (*Pinus* spp.)
Rhyncolus macrops Buch.	M, SA, cf (*Abies* spp., *Pseudotsuga* sp.)
Genus indet.	
Scolytidae	
Scolytus piceae (Sw.)	SA, M, cf (*Picea* spp.)
Dendroctonus cf. *brevicomis* LeC.	M, SA, cf (*Pinus* spp.)
Dendroctonus rufipennis (Kby.)	SA, M, cf (*Picea* spp.)

Taxon	Habitat and Ecological Requirements
Phloeotribus lecontei Schedl	SA, M, cf (Abies sp., Picea spp., Pseudotsuga sp.)
Polygraphus rufipennis (Kby.)	SA, M, cf (Picea spp., Abies spp., Pinus spp.)
Dryocoetes cf. affaber (Mann.)	SA, M, cf (Picea spp.)
Dryocoetes autographus Ratz.	SA, M, cf (Abies, Picea and Pinus spp.)
Dryocoetes sp.	
Pityophthous sp.	SA, M, cf
TRICHOPTERA	
Hydropsychidae	
Arctopsyche sp.	A, mtn, str.
Limnephilidae	
cf. Asynarchus sp.	A
cf. Clistoronia sp.	A, mtn. str., ponds
Dicosmoecus sp.	A, mtn. str.
cf. Limnephilus sp.	A
Limnephilinae genus indet.	

Taxon	Habitat and Ecological Requirements
Rhyacophilidae	
Himalopsyche sp.	A, mtn. str.
Rhyacophila sp.	A
HYMENOPTERA	
Formicidae	
Camponotus cf. *herculeanus* L.	M, SA, cf
Formica rufa cf. *marcida* Whlr.	M, SA
Myrmica (*Incompleta*) sp.	M, SA
Leptothorax (*Muscorum*) sp.	M, SA

Habitat Requirements:

A - aquatic

M - montane forests

SA - subalpine forests

T - alpine tundra

Ecological Requirements:

ch - on charred ground

cf - in coniferous forests,
host tree taxa in parantheses

d - in dung

mdw - in meadows

mtn. str. - in mountain streams

o - on open ground

r - riparian

sn - on snowfields

w - in wet biotopes, often in leaf litter

x - xerophilous

	Tree and Shrub							Herb									
	Abies	*Alnus*	*Betula*	*Juniperus*	*Picea*	*Pinus*	*Salix*	*Artemisia*	Cheno-Am	Compositae-Tubliflorae	Gramineae	Rosaceae	*Sarcobatus*	Cyperaceae*	Filicales	AP %	*Picea/Pinus*
Level 1	0.5	1	1		5	51	11	7	5	1	8.5	3		1	1	56.5	0.1
Level 2	3	3	1	1	6	46.5	11	6.5	5	1.5	5.5	3	1.5	4	1	55.5	0.13
$\bar{x}$	1.8	2	1	0.5	5.5	48.8	11	6.8	5	1.3	7	3	0.8	2.5	1	56	0.12

* Cyperaceae count not in total pollen sum

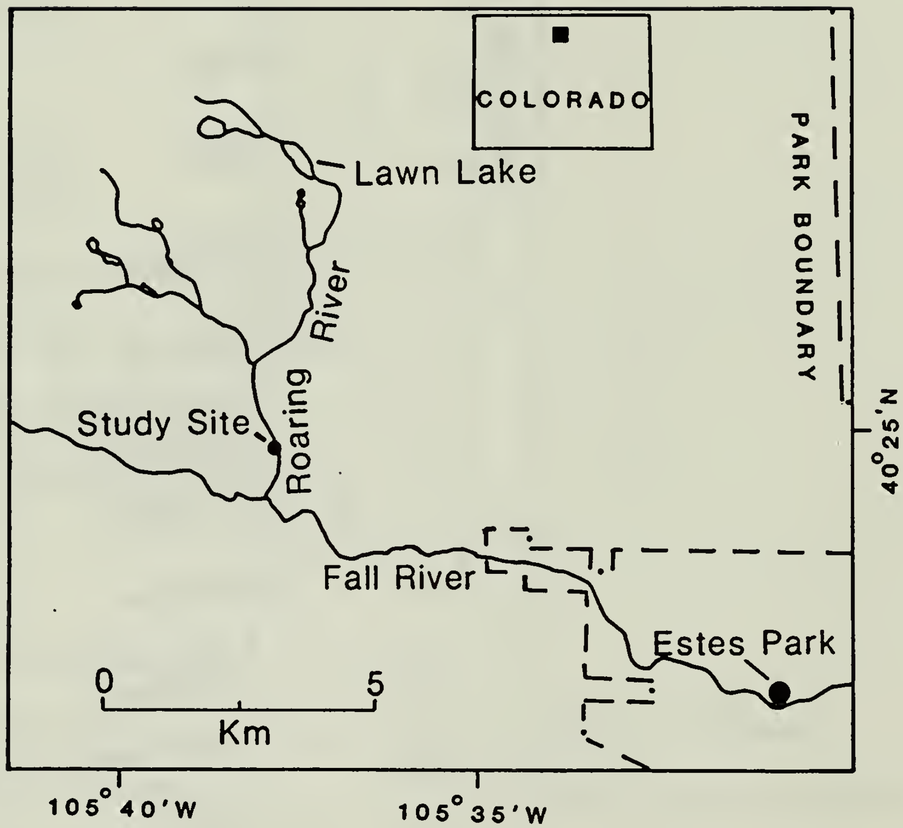
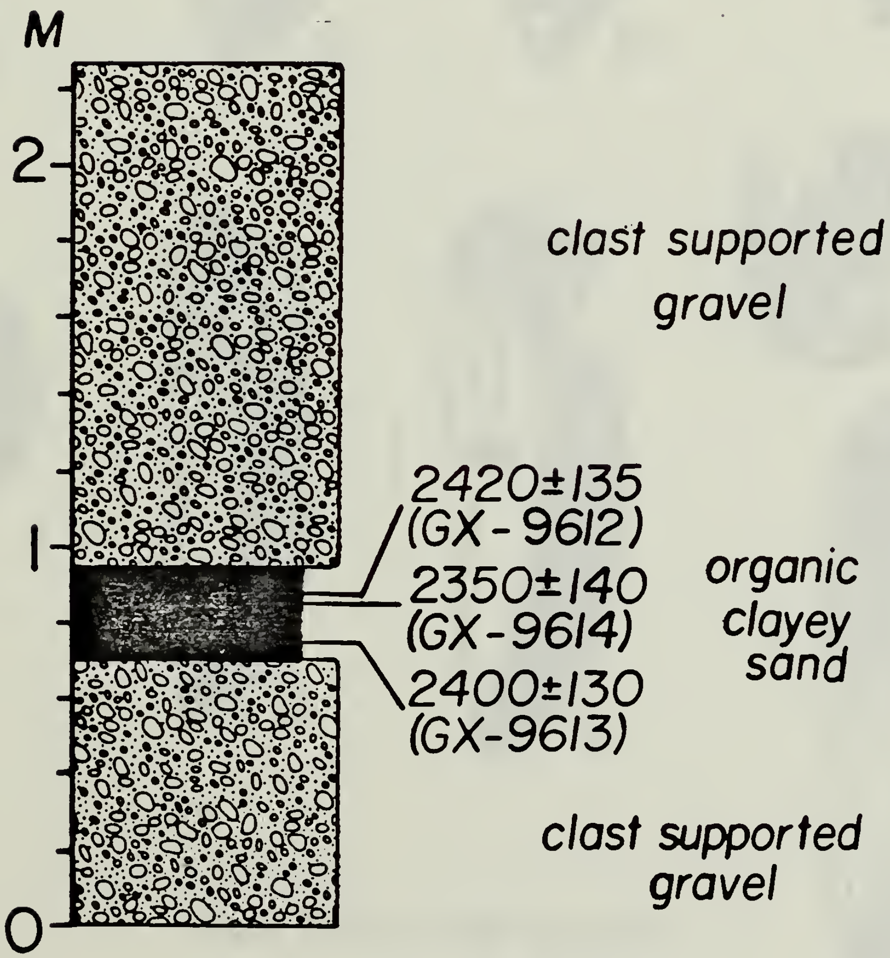

COLORADO
Lawn Lake
PARK BOUNDARY
Roaring River
Study Site
Fall River
Estes Park
0
5
Km
40°25'N
105°40'W
105°35'W

Fig. 1

ROARING RIVER SITE



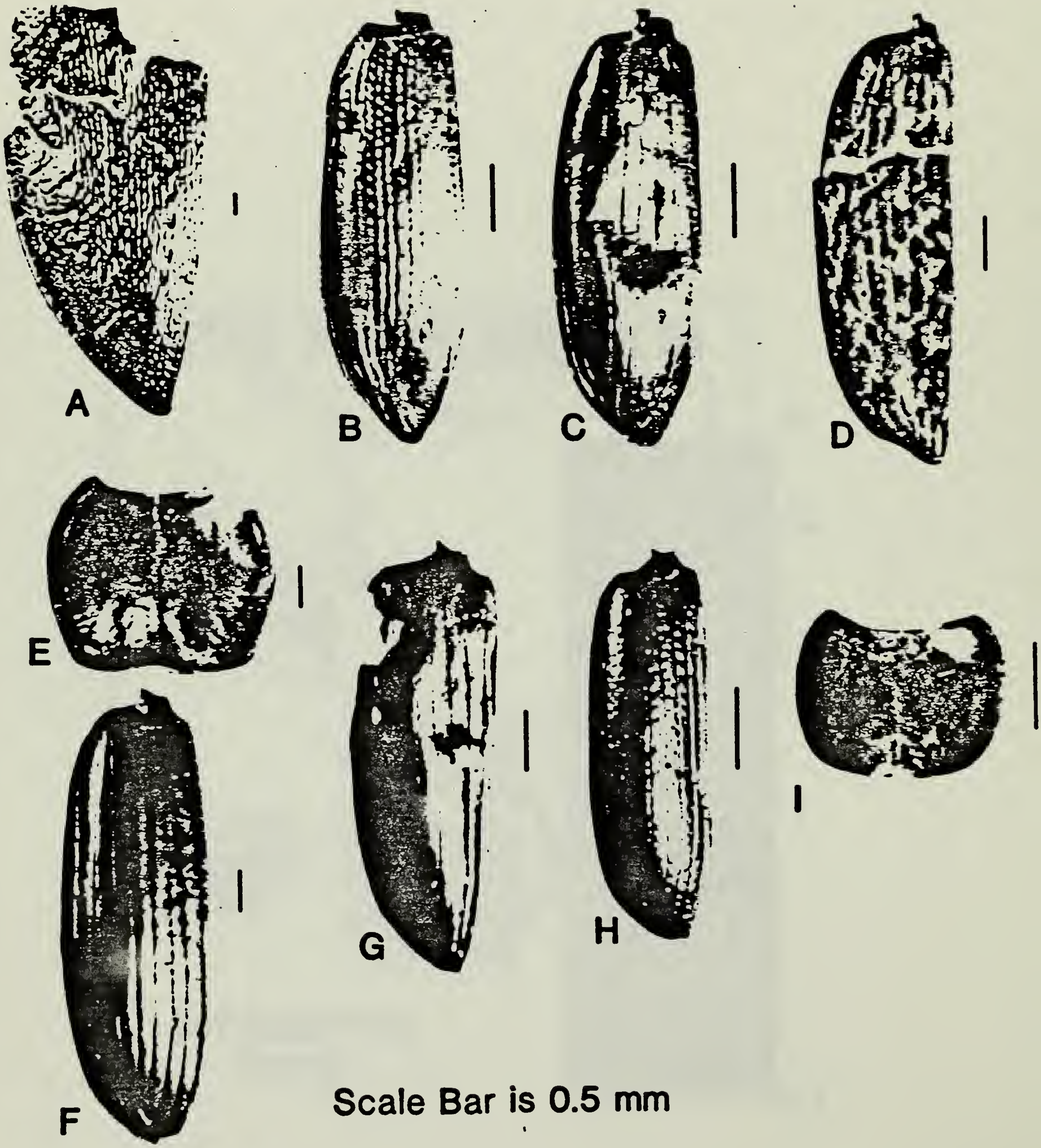


Fig 3

APPENDIX II

PALEOENVIRONMENTAL INTERPRETATIONS OF HOLOCENE INSECT FOSSIL ASSEMBLAGES FROM FOUR HIGH ALTITUDE SITES IN THE COLORADO FRONT RANGE, U.S.A.

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ABSTRACT

A series of four Holocene age sites in the Colorado Front Range form an altitudinal transect from subalpine forest to alpine tundra in the modern environment. Insect fossil assemblages from these sites have been analyzed for paleoenvironmental changes, including tree limit shifts. Tree limit altitudes have been inferred from the forest-tundra insect species ratios of the fossil assemblages, supplemented by plant macrofossil data.

A climatic optimum is suggested by maximal forest-tundra ratios between 9000 and about 7000 yr. BP. From 7000 to 4500 BP, the insect evidence suggests the continued nearby presence of conifers at the sites, as supported by the plant macrofossil record. Faunal evidence indicates a tree limit decline at 4500 BP. Declining forest-tundra insect ratios, combined with the conifer macrofossil record, suggest a climatic deterioration from 4500 to 3100 BP followed by a rapid amelioration, from 3000 to 2000 yr. BP. A gradual decline in the forest-tundra ratios occurred after 2000 BP, reaching 1:1 ratios at or before 1000 BP.

Broad similarities were found in the timing of Holocene changes with the insect fossil record from La Poudre Pass, and a north-south transect of Holocene paleobotanical sites from Alberta to southern Colorado.

INTRODUCTION

The aim of this study is to reconstruct the postglacial history of upper altitudinal treelimit in this part of the Colorado Front Range, based principally on fossil insect evidence. Four sites were chosen which are close to modern tree limit (i.e., the altitudinal tree species limit), and an underlying assumption of this work is that the forest - tundra ecotone will have shifted altitudes during the Holocene, in response to climatic changes. Thus, the fossil sites are assumed to be strategically situated to register insect faunal changes associated with tree limit shifts through the study site localities.

Lake Isabelle Sites

The two sampling sites in the Lake Isabelle basin lie about 1.5 km east of the Continental Divide, just west of the current lake shore, at altitudes of 3323 and 3325 m asl (Figure 1). The lake margin is in the subalpine forest - alpine tundra ecotone (Marr, 1967), and outlier islands of krummholz form trees (principally *Picea engelmannii*) extend to the two sites. The Lake Isabelle catchment basin is approximately 5.8 km^2 in area. Mean July temperature at the study site is about 10.5°C (Kiladis, unpublished report, 1980). Mean annual temperature is about 0°C, based on extrapolation from 30 years of temperature data from sites just to the south of the Isabelle basin (Losleben, 1983). Lake Isabelle is fed by meltwater from the Isabelle glacier from South St. Vrain Creek. An organic-rich deltaic deposit was discovered at the mouth of the creek during September 1981, when the lake water level was exceptionally low.

A short distance upstream from the deltaic site is a sedge meadow. A section of sedge peat was also sampled at this time. Sedge marsh

communities are prevalent along South St. Vrain Creek, between the Isabelle glacier and the upper limit of Lake Isabelle (Komarkova, 1979). Both the deltaic deposit and the sedge peat section have been radiometrically dated and analyzed for insect fossil remains.

Lefthand Reservoir

A peat bog lies at the upper end of the Lefthand Reservoir, 6.25 km east of the Continental Divide, at an altitude of 3224 m (Figure 1). The catchment basin area is approximately 5 km^2. The temperature regime at this site is nearly identical to that noted for the Lake Isabelle sites (Kiladis, unpublished report, 1980). The bog is bounded by subalpine forest on the north and west, by forest-tundra ecotone on the south and by the reservoir on the east. A section of sedge peat was sampled in 1978. Samples from the peat have been radiometrically dated and analyzed for insect fossils.

Mount Ida Ridge Pond

An isolated pond, less than 0.1 ha in size, is located about 1 km east of the Continental Divide in Rocky Mountain National Park on a broad plateau (Figure 2). The pond lies below Mount Ida Ridge, at an altitude of 3520 m asl, in the alpine tundra. The catchment basin is less than 1 km^2. Mean July temperature at the study site is about 9°C, and mean annual temperature about -2°C. The pond appears to be spring-fed, and is held back by a rock bar. Sedge peat has accumulated at the margins of the pond. A sediment core of this peat was collected during September, 1983. Samples from the sedge peat core have been radiometrically dated and analyzed for insect fossils.

METHODS

At the Lake Isabelle delta site, a 0.98 m section of sandy organic detritus was sampled from a cleaned face in the delta. The organic-rich material was so poorly consolidated that it did not lend itself to normal sampling procedures. Hence, instead of samples representing five cm intervals, samples ranging from 6 cm to 23 cm were collected. Two sets of samples were obtained for fossil insect and radiocarbon analyses. All of the samples were approximately 4 L in volume. Each sample was placed in a plastic bag, and transported to the laboratory for analysis.

The sedge peat section from west of Lake Isabelle was sampled from a cleaned face of 0.95 m depth. Blocks of peat, approximtely 10 cm deep, 15 cm wide, and 15 cm long were cut from the face, wrapped in aluminum foil and plastic, and transported to the laboratory for analysis.

The sedge peat section from west of Lefthand Reservoir was sampled in eight blocks, from the top of the peat down to 1.42 m depth. An additional 0.64 m of peat was sampled with a Russian corer, but not analyzed for insect fossils. Peat from the lowest 5 cm of the core was submitted for radiocarbon assay. The peat blocks were wrapped in aluminum foil and kept in cold storage.

At Mount Ida Ridge Pond, a 10 cm diameter plastic tube was pushed down into the sedge peat at the pond margin. A grussified bedrock base was encountered at a depth of 1 m, and the tube was then pulled out of the peat, and both ends sealed for transport back to the laboratory. All samples from

the four sites were kept in cold storage before subsampling. The range of sample sizes from the four sites is shown in Table 1.

The unconsolidated detrital samples from the deltaic deposit at Lake Isabelle were processed as bulk samples for insect fossil analyses. The contents of each sample bag were washed in a 300 μm mesh sieve, and the organic fraction isolated from the residual sands by gravity separation. Large twigs and cones in this organic fraction were removed and prepared for macrofossil identification and/or radiocarbon assay. The rest of the organic fraction was processed for insect fossils, using the kerosene flotation method (Coope, 1968) to concentrate and isolate the insect fossil fragments from the plant residue.

Peat blocks from the sedge peat sections above Lake Isabelle and from the Lefthand Reservoir site were subsampled in five or six cm intervals. The subsamples were soaked in a 5% NaOH solution to aid disaggregation, then washed in a 300 μm mesh sieve. The washed residue was then subjected to the kerosene flotation method.

The sediment core taken from Mount Ida Ridge Pond was extruded from the plastic tube, and sampled for insect fossils in 10 cm intervals. The entire core was used in the insect fossil analysis, with the exception of two samples taken for radiocarbon assay, and 1 cm^3 samples taken in 2-cm intervals for pollen analysis. The 10-cm intervals of peat were washed in a 300 μm mesh sieve, and the residues processed by the kerosene flotation method for extraction of insect fossils. The kerosene flotant of each sample from the four sites was washed in detergent, dehydrated in ethyl alcohol, and sorted under a low power stereo binocular microscope. Robust

fossil specimens of Coleoptera and Hymenoptera were mounted with gum tragacanth, a water soluable glue, onto modified micropaleontology cards. Fragile specimens and abundant replicate specimens were stored in vials of alcohol. Selected fossil larval sclerites of Trichoptera were mounted in polyvinyl lactophenol medium onto glass slides.

STRATIGRAPHY

Lake Isabelle, Delta Site (Fig. 3)

The basal organic detritus sample yielded a radiocarbon age of 6315 ± 70 yr BP. An additional radiocarbon assay, performed on wood samples from the 0.81 - 0.98 m depth of the section analyzed for insect fossils, has provided an averaged age of 9000 ± 285 yr BP. The interval 0.58 - 0.98 m consisted of sandy silts, containing less than 10% organic detritus by volume. Conifer needles and pieces of *Salix* (wilow) wood were recovered from samples in this interval. Samples taken from 0.38 - 0.58 m were sandy silts with less than thirty three 33% organic detritus by volume. The interval 0.35 - 0.40 m has yielded a radiocarbon age of 7830 ± 255 yr BP. The samples also contained conifer needles, spruce cones, and *Salix* wood. The interval between 0.21 and 0.38 m consisted of approximately equal volumes of sandy silt and organic detritus with wood fragments, conifer needles and spruce cones. The uppermost 0.21 m of samples consisted of organic detritus containing *Salix* wood, with less than one-third sandy silt. The interval 0.0 - 0.06 m yielded a radiocarbon age of 7975 ± 260 yr BP. This date falls within the standard deviation of the date on

material from 0.35 - 0.40 m. It appears that this upper portion of the section was deposited very rapidly, or perhaps in a single event. For the purpose of the fossil study, the upper 0.40 m of the section is treated as a bulk sample with an averaged age of 7900 yr BP.

Lake Isabelle, Sedge Peat Site (Fig. 4)

The basal 0.1 m of this site (0.85 - 0.95) has been dated at 7080 ± 90 yr. B.P. This interval contained at least two thirds sand by volume, mixed with poorly humified sedge peat and conifer needles. Between 0.60 and 0.85 m, poorly humified sedge peat with less than one third sand was found. A few fragments of wood were also found in this interval (Fig. 6), but no conifer needles. Well humified peat was found in the sampling intervals between 0.15 and 0.60 m. A radiocarbon age of 1495 ± 130 yr. B.P. has been assigned to the interval 0.16 - 0.18 m. The uppermost 0.15 m of the peat from this site is poorly humified, with less than one third sand by volume.

Lefthand Reservoir Site (Fig. 5)

Sedge peat was sampled from a bank at water's edge down to a depth of 2.06 m. The upper 1.42 m of peat was sampled in eight monolithic blocks, and the lower 0.64 m was sampled using a Russian peat corer. Basal sediments of sand and coarse pebbles were reached with the corer, and the interval 2.05 - 2.06 m has yielded a radiocarbon age of 7760 ± 160 yr. B.P. (DIC-1338). The upper 1.42 m peat block have been analyzed for macrofossils; the stratigraphy is shown in Fig. 5.

As an experiment, a sample of peat from the interval 1.34 - 1.42 m was processed by the kerosine flotation method for extraction of insect fossils, and then the residue underwent radiocarbon assay, yielding an age of 900 ± 150 yr. B.P. An interpolated age of 5350 yr BP was derived for the depth, 1.42 m, based on assumed uniform peat accumulation rates from 7760 yr BP (the base of the section at 2.06 m) to the uppermost 5 cm, which has yielded a radiocarbon age within the modern standard of activity. Since the kerosened peat residue from the 1.32 - 1.42 m interval was contaminated with several organic compounds, the radiocarbon date obtained is extremely suspect. The interpolated age of 5350 yr BP is considered the only reliable estimate of the actual age of this interval.

Fine fibered sedge peat, containing numerous conifer needles and cones, as well as _Salix_ wood, was found between 0.70 and 1.42 m. Coarse fibered sedge peat dominated the upper 0.7 m, with conifer needles and _Salix_ wood at several intervals.

Mount Ida Ridge Pond Site (Fig. 6)

Compaction of the approximately 1 m core collected in the field, resulted in only 0.60 m of core when extruded in the laboratory. A radiocarbon assay of a peat lens between 0.50 and 0.55 m provided a basal date of 9070 ± 175 yr BP. Beneath this peaty lens was an additional 0.10 m of micaceous sandy gravel with subangular cobbles. Between 0.20 and 0.50 m is a fine-fibered sedge peat with conifer needles, cones and _Salix_ wood in the lower 0.10 m. The peat occurring between 0.25 and 0.30 m depth was removed from the core before processing for insect fossils, and yielded a radiocarbon age of 8340 ± 310 yr BP. The interval 0.1 - 0.2 m consisted of

sedge peat with coarser fibers, and the uppermost 0.1 m of the core contained fine fibered sedges. The interval, 0.01-0.06 m yielded a radiocarbon age of 4600 ± 210 yr BP. Each 0.1 m interval sampled for insect fossils contained less than 1 L of sediment (less than a quarter of the volume of the samples from the Lake Isabelle sites), and accordingly yielded far fewer insect fossils.

FOSSIL INSECT ASSEMBLAGES, LAKE ISABELLE DELTA AND PEAT SITES

The delta site produced the greatest number of fossil insect specimens of the four sites discussed. A minimum of 3050 individual fossil insects are represented. The insect faunal list, excluding Trichoptera, includes 136 insect taxa from 25 beetle families in addition to five ant taxa and parasitic Hymenoptera (Table 2).[1] Sixty-six specific identifications were made from the above fauna (49%). Fossil insect assemblages from the deltaic deposit represent a number of biological communities and distribution patterns. A discussion of selected taxa is presented below.

In contrast to the deltaic deposit, all levels of the sedge peat from Lake Isabelle yielded only 36 insect fossil taxa, representing a minimum of 377 individuals. These taxa, including the 15 specific determinations, are a subset of the faunal list from the deltaic deposit (Table 2).

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[1]Complete tabulations of the minimum number of individuals of the insect taxa from each of the four sites is available, upon request, from the editor.
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Open Ground Fauna

A number of the insect species in the Lake Isabelle sites are presently found in open ground habitats, either on the alpine tundra or in open ground situations in the subalpine forest zone. The ground beetle, Notiophilus directus is such a species. Notiophilus directus is found today on bare ground, in spots with tiny mosses, frequently along streams. This beetle is a Rocky Mountain inhabitant that is rarely collected. Lindroth (1961) records N. directus from British Columbia and Alberta, stating that it is not a pronounced mountain species, whereas Edwards (1975) found specimens at various mountain localities in Glacier National Park, Montana, including three localities above tree limit.

Another ground beetle, Trechus chalybeus, is found today in the Rocky Mountains from Idaho and Montana to New Mexico (Lindroth, 1961). This beetle is relatively hygrophilous, often found among leaf litter of willow and alder as well as in wet moss and also occurrs regularly above tree limit at the margin of snow patches. Its near relative, Trechus coloradensis (Fig. 7, A) apparently has very similar ecological requirements and modern distribution. The carabid beetle, Bembidion grapei is found today on dry, gravelly localities where vegetation is sparse. Bembidion grapei has a transamerican distribution in the boreal forest and in arctic and alpine regions (Lindroth, 1963). Pterostichus surgens is a flightless species of ground beetle, for the most part known to inhabit the alpine meadows of the Rocky Mountain region (Fig. 8, A). Other carabid beetles that are commonly associated with open ground environments include Amara cf. pallipes and Trichocellus mannerheimi. Amara pallipes is a transamerican species today, living in open meadows as far south as the mid-west (Lindroth, 1968); it has

also been found on a bare ridge surrounded by snowfields in Glacier National Park (Edwards, 1975). Trichocellus mannerheimi (Fig. 7, C) is found across North America in the boreal and arctic regions, and has an isolated population in Colorado (Fig. 8, B). This beetle has been found between 3050 and 3350 m asl in Colorado, and is generally associated with dry slopes on sandy till with sparse, low vegetation (Lindroth, 1968).

Several of the staphylinid (rove) beetles found in the Lake Isabelle sites are associated with open ground, treeless habitats. Acidota quadrata is a flightless species with boreal and arctic-alpine distribution (Fig. 8, C). In Colorado it has been found at or above tree limit, commonly among alder (Alnus) and willow (Salix) leaf litter, near streams and near snowfields, or on wet mosses in the alpine tundra (Campbell, 1982). Tachinus elongatus (Fig. 7, E) is another rove beetle that is normally considered as a boreo-montane species, except in Colorado, where it has been found in the alpine zone, at 3660 m asl, in Rocky Mountain National Park (Campbell, 1973). Tachinus angustatus is also frequently found above tree limit in the Rockies, often on snowbanks (Campbell, 1973).

Finally, the scarab beetle, Aegialia lacustris is associated with open ground environments in the Rocky Mountains. Aegialia lacustris was taken from both the subalpine and alpine regions in the Medicine Bow Mountains (Blake, 1945) and I have collected it above treeline, among grass roots in sandy soil, at Loveland Pass (Elias, 1983).

Subalpine Forest - Alpine Tundra Ecotone Fauna

Many of the species from the Lake Isabelle assemblages are found both in the alpine tundra and upper subalpine forest regions in the Rockies.

Their presence in the fossil record is therefore somewhat ecologically ambiguous, but signifies the close proximity of the forest-tundra ecotone to the site. Among these taxa are the ground beetles, Patrobus septentrionis and Pterostichus sphordrinus. Patrobus septentrionis is a holarctic species, occurring in the boreal and subarctic of North America, with isolated populations in the Colorado Rockies. This beetle is often found at the border of standing or slow moving water, with abundant grasses and sedges. While it is a member of the alpine fauna of Europe, it apparently does not live above tree limit in North American mountains (Lindroth, 1961). Pterastichus sphodrinus lives today in the montane and subalpine forests of the Rockies, and above treelimit, at least in Glacier National Park (Edwards, 1975).

The four species of the ground beetle Nebria which occurred in the deltaic deposit are all found in the Lake Isabelle region today (D.H. Kavanaugh, written comm., 1984). Nebria purpurata and N. arkansana are more or less restricted to the edges of streams, while N. gyllenhali and N. trifaria may be found at considerable distances from water, at least at higher altitudes (Kavanaugh, D.H., 1984; Kavanaugh and Martinko, 1972). Nebria generally are adapted for running across snow surfaces in summer, where they prey on a variety of insects which have fallen onto the snow.

Several of the staphylinid species from the Lake Isabelle sites also range above tree limit in their modern Rocky Mountain distributions. Eucnescosum brunnescens and E. tenue are both associated with moist habitats (often leaf litter) in the alpine and subalpine regions (Campbell, 1984). Olophrum consimile is a transamerican species associated with alpine and subalpine forest regions, and is an inhabitant of leaf litter (especially of

alder and willow), as well as pondmargins, clumps of mosses and sedges. Olophrum rotundicolle (Fig. 8, D) has a very similar modern distribution and set of ecological requirements, with the exception that it is not known from Colorado today (Campbell, 1983).

The dung beetle, Aphodius wickhami, is also currently found in the Lake Isabelle basin. This species is very common at high altitudes in the Colordo Front Range, and is commonly found in sheep dung (R.D. Gordon, written communication, 1983). In the sedge peat from Lake Isabelle, fossil parts of adults and larval head capsules of A. wickhami were found in most levels. In the uppermost 5 cm of the sedge peat, whole larvae of this species were found, intact.

The ant, Formica neorufibarbis is found today in the upper subalpine zone of the Rockies, and just beyond the forest-tundra ecotone. Formica neorufibarbis has been taken from several high altitude localities in Colorado (Francoeur, 1973), and is apparently the most cold-adapted species of Formica in North America.

Subalpine Forest Fauna

The subalpine forest fauna is likewise well represented in the two faunal lists from the Lake Isabelle basin. Table 3 shows the relationships between certain of the subalpine forest beetle species from the Lake Isabelle assemblages and their host trees. The majority of tree-associated beetle taxa from these sites are known to attack either Abies lasiocarpa Picea engelmannii, or both. Some of the host trees associated with the fossil bark beetles are found in the montane forest regions of the Rockies (altitudes below 2750 m), but the presence of these beetle species in these

assemblages is probably due to wind-transported specimens, carried upslope by as much as 1000 m and deposited in the Lake Isabelle cirque basin. The colydiid genus, Lasconotus (Fig. 7, F), is usually found in association with bark beetles of the genera Pityophthorus and Phloeosinus (Kraus, 1912).

Among the subalpine forest associated beetle taxa which live on the forest floor and have no direct host-parasite relationship with the trees are the following species. The ground beetle, Calathus advena is a boreo-montane species which is found mostly in very shady localities, among leaf litter and debris. The staphylinid beetle, Micropeplus laticollis (Fig. 7, D) is a widely distributed boreo-montane species, commonly found in conifer needle litter under Engelmann spruce, subalpine fir, ponderosa pine (Pinus ponderosa) and lodgepole (Pinus contorta) pine. This beetle has also been found inhabiting squirrel middens (Campbell, 1968). Another staphylinid, Tachyporus borealis, lives today in Colorado up to tree limit, and is also associated with coniferous needle litter (Campbell, 1979).

Marsh or Bog and Aquatic Fauna

Besides such species as Olophrum consimile and O. rotundicolle, a number of other species from the Lake Isabelle basin sites are found living in mosses or sedges at the edge of marshes or bogs. These include the ground beetles, Pterostichus patruelis and Agonum affine. Pterostichus patruelis is a eurytopic swamp species, found especially in Sphagnum bogs, but also in sedge mires (Lindroth, 1966). This species occurs today across the northern parts of North America, with smaller populations ranging south at least to Kansas and Colorado. Agonum affine (Fig. 7, B) is a boreo-montane species, found at the border of ponds and swamps which have

dense sedges and mosses. In Boulder County, this species has been taken from the montane zone, but not yet from the subalpine (Armin, 1963). Many of the beetles represented in the Lake Isabelle basin sites live in open water, including most of the species from the families Dytiscidae, Hydrophilidae and Hydraenidae.

The elmid fossil and the dryopid beetle, Helichus are associated with running water, and may have lived in South St. Vrain Creek, above the delta.

Numerous caddisfly larval fossils were recovered from the Lake Isabelle assemblages, but have not been identified.

FOSSIL INSECT ASSEMBLAGES, LEFTHAND RESERVOIR

The sedge peat section from this site (Table 2) produced a minimum of 591 individual insects, representing 49 taxa, all but five of which were also found in the Lake Isabelle delta assemblages. The carabid beetle, Bembidion constricticolle, is a riparian species, apparently confined to montane and subalpine stream banks in the western parts of North America (Lindroth, 1963). The bark beetle, Scierus pubescens, is a western North American species, known to attack stumps, lower bole and roots of rather large, postrate Picea engelmannii and Abies lasiocarpa (Wood, 1982). Larvae of the caddifly genus Agrypnia live in lakes, marshes and slow rivers in northern and montane regions of the Holarctic (Wiggins, 1977).

FOSSIL INSECT ASSEMBLAGES, MOUNT IDA RIDGE POND

The core of the sedge peat from this small pond yielded a small number of insect fossils (a maximum of 267 individuals), representing 40 insect and crustacean taxa, including 14 specific determinations (Table 2). The great majority of taxa from this site have been previously described from the Lake Isabelle basin sites with the following exceptions.

The ground beetle, Selenophorus planipennis is an inhabitant of the North American interior, from south central Canada south to Arizona and Colorado (Lindroth, 1968). This species has been found only on the eastern plains and in the foothills of the Front Range in Boulder County, Colorado, on dry sandy soil with sparse vegetation (Armin, 1963). Selenophorus planipennis is a fully winged beetle, and hence its presence in Mount Ida Ridge Pond sediments may represent upslope wind transport of a straggler from the foothills east of Rocky Mountain National Park.

The leaf beetle, Plateumaris flavipes occurs farther north than any other species in the subfamily Donaciinae (I.S. Askevold, written communication, 1984). Plateumaris flavipes also occurs in the Rocky Mountains, as far south as Colorado, but probably does not live in the true alpine tundra. This beetle has been collected from sedges. The Donaciines as a group feed on emergent vegetation in slow moving or standing water.

The ant, Formica fusca subaenescens is a boreo-montane subspecies occurring across North America. This ant has been found in Colorado, up to an altitude of 3000 m., and so it forms a part of the subalpine forest insect fauna (Francoeur, 1973). All of the head capsules of this ant that were found in the Mount Ida Ridge Pond sediments were of the worker caste, which is flightless.

DISCUSSION

As noted in previous Rocky Mountain fossil insect studies (Elias, 1982, 1983), the presence of bark beetle (Scolytidae) and other tree-associated species in high altitude deposits may well be due to upslope wind transport. The presence of wind carried insects of many orders has been recorded from most of the world's mountain chains (Mani, 1968). Dead or torpid bark beetles, in particular, have been collected from snowfields in the Cascade Mountains (Furniss and Furniss, 1972), the White Mountains of New Hampshire (Darlington, 1943) and the Rocky Mountains of Montana (Chapman, 1954) and Colorado (Caudell, 1909). Bark beetles may be caught up by convection wind currents on warm, summer days, and carried to high altitudes where they drop to the surface after folding their wings in response to contact with cold air. Under certain conditions, bark beetles may be carried 30 km or more from their source. Furniss and Furniss (1972) collected 26 scolytid species above treeline in Oregon and Washington. Especially in the deltaic deposit at Lake Isabelle, numerous bark beetle specimens may have been blown into the cirque basin and subsequently deposited at the delta site by rains or snow meltwater. Because of this phenomenon, special constrictions have been placed on the interpretations of the bark beetle data from the four sites.

Zoogeographical Implications

Of the 70 species identified from the four fossil sites, 39, or 56%, have modern distributions in the boreo-montane regions of North America. Seventeen species (24%) are now restricted to the montane and alpine regions

of the western North American mountain ranges. Many of the remaining insect species on the faunal lists have modern distributions which are poorly known, and a few, like *Hippodamia convergens*, are cosmopolitan in North America. The ground beetles, *Patrobus septentrionis* and *Trichocellus mannerheimi* are essentially boreo-arctic species, with isolated populations in the Colorado Rockies. Modern specimens of the staphylinid, *Olophrum rotundicolle* have yet to be found in Colorado, or in any of the Rocky Mountain ranges in the United States (Fig. 8, D). Fossils of *Olophrum rotundicolle* have been found in peat from the La Poudre Pass site, in assemblages ranging in age from about 8800 yr BP to nearly modern (Elias, 1983, 1984). It would appear likely that at least small populations of this beetle are still present in Colorado, but perhaps only in high altitude bogs or sedge marshes. For the most part, however, the insect species in the four fossil sites are found today in close proximity to the fossil sites.

Faunal Diversity of Allochthonous vs. Authochthonous Assemblages

The deltaic deposit from Lake Isabelle represents a set of allochthonous assemblages, that is, assemblages of fossils not derived strictly from the immediate vicinity of the site, but carried to the site by a stream and by wind. The faunal diversity of the deltaic deposit is roughly three times that of the other sites, which are autochthonous peats. A review of Quaternary insect fossils in autochthonous and allochthonous assemblages from 18 other North American sites reveals that allochthonous assemblages average twice as many insect fossil taxa as autochthonous ones (Elias, ms. in prep.). The Lake Isabelle delta assemblages appear to reflect the regional insect fauna of their times, especially that of the

Isabelle catchment basin, whereas the peat assemblages from Lake Isabelle, as well as the Lefthand Reservoir and Mount Ida Ridge Pond peats, appear to be dominated by taxa which are commonly found in sedge fen habitats. The degree to which such sedge peat faunas represent strictly autochthonous deposition is quite variable from site to site, and cannot be easily discerned from modern field observations. Sedge peat from La Poudre Pass formed in apparently similar topographic and hydrologic settings as the Lefthand Reservoir and Mount Ida Ridge Pond peats, and yet the La Poudre Pass peats have yielded 83 insect taxa, compared with 48 and 36 taxa from the other two sites, respectively.

PALEOENVIRONMENTAL INTERPRETATIONS

Lake Isabelle Sites

The combined information from the two Lake Isabelle sites provides a reconstruction of paleoenvironments of this basin from 9000 yr. BP to 500 yr. BP, with a depositional gap between the two sites from 8000 and 7000 yr. BP (Fig. 9). The fossil assemblages from the deltaic deposit indicate the nearby presence of trees between 9000 and 8000 yr BP. The ratios of forest-to-tundra species based on the number of identified species from the delta assemblages would suggest that tree limit was higher than present during this interval, whereas the more conservative set of ratios (which excludes bark beetles and other flying taxa) indicates at least one major tree limit oscillation in the same period. The most reliable estimate of the forest-tundra species ratios undoubtedly lies between the two sets of ratios shown, as is true for all the sets of ratios shown in Figure 9.

However, since the proportion of wind-carried beetles in each of the faunal assemblages was probably quite variable through the time of deposition, the only viable approach would appear to be to plot both sets of ratios, as maximum and minimum estimates of past tree limit positions. In the forest-tundra ecotone regions of the Front Range, preliminary data from the collection of modern beetles suggests that subalpine forest and alpine tundra faunal elements are nearly equally represented (Elias, unpublished data, 1984). Thus the ratio of forest to tundra species from this ecotone should also be close to 1:1 in the fossil record, unless differential preservation has somehow biased the record.

Relatively high tree limits from 7000 to about 4500 yr BP are suggested by the "all species" ratios from the Lake Isabelle peat assemblages. Following this, a remarkably constant forest-to-tundra species ratio is found in all subsequent assemblages. This, combined with a lack of conifer macrofossils in most of this interval, suggests that the sedge meadow above Lake Isabelle became very stable, or perhaps expanded, during the past 4500 yr, to the exclusion of the coniferous forest. Whether this vegetational stability was due to climatic, edaphic or biological factors remains unknown. The seeming complacency of the fossil insect record from this interval allows little paleoenvironmental interpretation, but perhaps is suggestive of climatic conditions cooler than the 7000 to 4500 yr BP period, and either cooler than or similar to modern levels. A Holocene climatic optimum at Lake Isabelle apparently began by at least 8000 yr BP, if not earlier, and lasted until about 5000 BP.

Lefthand Reservoir

The studied fossil insect record at Lefthand Reservoir begins just before 5000 yr. BP., and thus provides information only on the latter half of the Holocene. A gradual climatic deterioration is observed from the oldest level (ca. 5350 yr BP) to 3500 yr BP, followed by a brief amelioration (maximum forest-tundra species ratios in the "all species" curve). That tree limits were depressed between about 4300 and 3100 yr BP at this site is suggested not only by the fossil insect record, but also by the disappearance of conifer macrofossils during this interval. Increases in the numbers of bark beetles, combined with the reappearance of conifer needles at 3100 yr BP, suggests a brief climatic amelioration at this time. Another climatic deterioration, perhaps not as severe as this one, apparently began by about 2800 yr BP, followed by some additional small-scale oscillations culminating in relatively cold climatic conditions within the past few centuries.

Mount Ida Ridge Pond

The small sample sizes and degree of uncertainty concerning the radiocarbon chronology from this site make the paleoenvironmental interpretations more tentative than the other sites. The two sets of forest-tundra species ratios are very close together (Fig. 10), due to the small number of flying beetles in the assemblages. Between 9000 and 8300 yr BP, the forest-tundra species ratios suggest that conditions were similar to today, with tree limit downslope from the site. An apparent climatic optimum was reached, probably within a few centuries after 8300 yr BP. Tree limit may have advanced to the altitude of Mount Ida Ridge Pond, however, there is no conifer macrofossil evidence to suggest that trees colonized the

immediate vicinity. Modern tree limit in Rocky Mountain National Park is approximately 50 m downslope from the pond, but numerous dead, standing tree stumps have been found above modern tree limit at altitudes up to that of the pond site. Recent studies employing radiocarbon assays of heartwood from some of these dead stumps indicate that higher tree limits were attained in this region several hundred years ago (Nichols, unpublished data, 1984).

It is clear that additional fossil insect studies will be required before a precise chronology of Holocene events can be drawn for the Rocky Montain region. Local hydrological changes and ecological succession at the study sites have influenced the fossil insect assemblages to an unknown but certainly considerable degree in some cases, and numerous replicate studies within this region will serve to separate local effects from the regional paleoenvironmental signal.

Comparisons With Other Rocky Mountain Studies

The only other Holocene insect fossil study published from the Rocky Mountain region is the La Poudre Pass site (Elias, 1983, 1984). The paleoenvironmental reconstruction from this site, based on forest-to-tundra species ratios, is shown in Figure 9. A Holocene climatic optimum and accompanying higher tree limit is inferred for the interval 8800 - 4500 yr BP. Tree limit depression and climatic deterioration in this region are suggested by the insect and conifer macrofossil record from about 4500 - 3000 yr BP, with trees distant from the site from 4500 to about 1900 yr BP. Climatic warming probably began around 3000 yr BP, and continued until about 1800 yr BP, followed by another climatic deterioration.

Additional comparisons can be made with paleobotanical studies of Rocky Mountain sites from Jasper, Alberta, to the La Plata Mountains, southern Colorado (Fig. 11). A survey of the paleoenvironmental chronologies from these sites reveals broad patterns of similarity in climatic and tree limit changes, with a few notable exceptions. Early Holocene climatic optima are noted from all of the studies, except Maher's (1972) Redrock Lake investigation. The timing of the commencement of climatic warming to levels greater than modern values ranges from 9600 yr BP at Lake Emma, Colorado to 7100 yr BP at the Kootenai River site, Montana. A mean date from all of the sites (excluding Redrock Lake) is 8800 yr BP, which agrees closely with the chronologies from La Poudre Pass, the Lake Isabelle sites and Mount Ida Ridge Pond. Deposits of rock glaciers in the Fourth of July Valley cirque, Benedict's (1981) "Ptarmigan advance," are reported to be older than about 6300 yr BP and younger than 9200 yr BP. Beget (1983) cites other paleoenvironmental data from the Rocky Mountains and elsewhere as indicative of an early Holocene climatic cooling, probably between 8500 and 7500 yr BP. No evidence for a climatic deterioration is apparent in the Front Range insect fossil record of this interval. The climatic deterioration marking the close of the climatic optimum phase is asynchronous along the Rocky Mountain sites studied. The oldest date for this event is 5200 yr BP, from the Jasper, Alberta study. The youngest date is 3000 yr BP, from Lake Emma, Colorado, although the sites from intermediate latitudes show no north-south chronological trend. The mean age from eight sites is 4300 yr BP, again, agreeing quite well with the chronologies from the Colorado fossil insect studies.

Most of the studies suggest that climatic deterioration has occurred in

the Rocky Mountain region within the last thousand years, accompanied by a general depression in tree limits. Maher's (1972) interpretation of pollen from Redrock Lake is out of phase not only with the fossil insect interpretations from Front Range Sites, but also with all of the other pollen study interpretations shown of Figure 11 from the Rockies. Several authors have suggested that Maher's interpretation of _Pinus/Picea_ ratios from the Redrock Lake samples may be in error, since comparisons with the modern regional pollen spectra suggest that a general lowering of tree limits and climtic cooling have taken place there in the past 5000 years (Hall, 1977; Nichols, 1982; Kearney and Luckman, 1983a).

The depositional records of the four sites are incomplete for the Holocene, but allow some tentative reconstructions for the Front Range, when taken together. Trees reached modern altitudinal limits between 9500 and 9000 yr BP, and climatic conditions were probably already as warm as today by that time. A Holocene climatic optimum with elevated tree limits occurred between about 8500 and 5000 yr BP. A sharp climatic deterioration followed, from 4500 to about 3000 yr BP. After this, the timing of climatic events becomes less clear in the fossil insect record, but an amelioration apparently ensued after 3000 yr BP, and the climate cooled once again within the past 2000 yr.

ACKNOWLEDGMENTS

Drs. H. Nichols, S. K. Short, G. H. Miller, and J. T. Andrews, University of Colorado, Institute of Arctic and Alpine Research, assisted in the collection of samples for this study, as did other colleagues from

INSTAAR. I also thank Nichols and Short for their comments and suggestions throughout the study. Identifications of beetle fossils were made by Drs. Campbell, Bright, Becker and Smetana, Biosystematics Research Institute, Ottawa, and Dr. J. V. Matthews, Jr., Energy Mines and Resources, Canada. Dr. A. Francoeur, University of Quebec at Chicoutimi, identified ant fossils and Bridget Wilkinson, London, England, identified caddis larval fossils. Scanning electron micrographs of fossil specimens were taken at the U.S. Geological Survey, Denver Federal Center, with the assistance of P. E. Carrara and J. Nishi. Financial support for this study was provided by a grant from the National Park Service, CX-1200-2-B048, for paleoecological research in Rocky Mountain National Park, and by the National Science Foundation, Long-Term Ecological Research, BSR-8012095.

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Figure Captions

Figure 1. Map of the upper South St. Vrain Creek drainage, showing study sites above Lake Isabelle and Lefthand Reservoir. Vegetation zones after Hansen-Bristow, 1981.

Figure 2. Map of the Mount Ida Ridge region, Rocky Mountain National Park, showing the pond from which samples were obtained, as well as the La Poudre Pass site, also discussed in text.

Figure 3. Stratigraphic section, Lake Isabelle Delta site. w - wood fragments, n - conifer needles, c - spruce cones.

Figure 4. Stratigraphic section, Lake Isabelle peat site. w - wood fragments.

Figure 5. Stratigraphic section, Lefthand Reservoir site. w-wood fragments, n-conifer needles, cn-charred conifer needles, c-spruce cones.

Figure 6. Stratigraphic section, Mount Ida Ridge Pond site. n - conifer needles, c - spruce cone, w - wood fragments.

Figure 7. Scanning electron micrographs of insect fossils from the Lake Isabelle Delta site. A - Left elytron of Trechus coloradensis, B - Pronotum of Agonum affine, C - Pronotum of Trichocellus mannerheimi, D - Left elytron of Micropeplus laticollis, E - Eighth abdominal tergite of Tachinus elongatus (female), F - Right elytron of Lasconotus sp., G - Head and pronotum of Stephanopachys sobrinus, H - Left elytron of Dendroctonus sp., I - Pronotum of Cryphalus ruficollis, J - Right elytron of C. ruficollis.

Figure 8. Known modern North American distributions of species from the study sites. A - Pterostichus surgens, B - Trichocellus mannerheimi, C - Acidota quadrata, D - Olophrum rotundicolle.

Figure 9. Ratios of forest dwelling to alpine tundra dwelling beetle species from the Lake Isabelle and Lefthand Reservoir sites, compared with the La Poudre Pass site (after Elias, 1984).

Figure 10. Ratios of forest dwelling to alpine tundra dwelling beetle species from the Mount Ida Ridge Pond site.

Figure 11. Comparison of Holocene paleoenvironmental chronologies along a north-south transect of the Rocky Mountain region. Sites range in latitude from Jasper, Alberta (52° 55'N) to the La Plata Mountains, Colorado (37° 28'N). Comparative terms for each site sequence are read from the bottom, upwards.

Table Titles

List of Arthropod Taxa from Four Holocene Sites in the Colorado Front Range

Taxon	Lake Isabelle Delta Site	Lake Isabelle Peat Site	Lefthand Reservoir	Mt. Ida Ridge Pond
INSECTA				
COLEOPTERA				
Carabidae				
Trachypachus holmbergi Mnnh.	+	-	-	-
Nebria arkansana arkansana Csy.	+	-	-	-
Nebria gyllenhali Schnhr.	+	-	-	-
Nebria purpurata LeC.	+	-	-	-
Nebria trifaria LeC.	+	-	-	-
Nebria trifaria pasqueneli Kav.	+	-	-	-
Notiophilus directus Csy.	+	-	-	-
Patrobus septentrionis Dej.	+	+	+	+
Trechus coloradensis Schffr.	+	+	+	-
Trechus chalybeus Dej.	+	-	-	-
Bembidion coradatum LeC.	+	-	-	-
Bembidion grapei Gyll.	+	-	-	-
Bembidion (*Incertum*) sp.	+	-	-	-
Bembidion rapidium LeC.	+	-	-	-
Bembidion constricticolle Hayw.	-	-	+	-
Bembidion spp.	+	+	-	-
Pterostichus patruelis Dej.	+	-	-	-
Pterostichus sphodrinus LeC.	+	-	-	-
Pterostichus surgens LeC.	+	-	+	-
Pterostichus spp.	+	+	+	-
Calathus advena LeC.	+	-	-	-
Agonum affine Kby.	+	-	-	-
Agonum spp.	+	-	-	-
Amara cf. *pallipes* Kby.	+	-	-	-
Amara spp.	+	-	-	-
Selenophorus planipennis LeC.	-	-	-	+
Anisodactylus lugubris Dej.	+	-	-	-
Trichocellus mannerheimi Dej.	+	-	-	-
Dytiscidae				
Hydroporus (*vilis*) sp.	+	-	-	-
Hydroporus (s. str.) sp.	-	+	-	-
Hydroporus sp.	+	+	-	+
Agabus austini sharp	+	-	-	-
Agabus tristis Aubé	+	-	-	-
Agabus sp.	+	-	-	+
Genus indet.	+	-	-	-
Hydrophilidae				
Helophorus spp.	+	-	+	-
Hydrobius fuscipes L.	+	-	-	-
Hydrobius sp.	+	-	-	-
Enochrus sp.	+	-	+	-
Cercyon sp.	+	-	-	-
Genus indet.	+	-	-	

List of Arthropod Taxa from Four Holocene Sites in the Colorado Front Range

Taxon	Lake Isabelle Delta Site	Lake Isabelle Peat Site	Lefthand Reservoir	Mt. Ida Ridge Pond
Hydraenidae				
Hydraena sp.	+	+	-	
Staphylinidae				
Micropeplus laticollis Makl.	+	-	-	
Oxytelus sp.	+	-	-	-
Oxytelini sp.	+	-	-	-
Bledius sp.	+	-	-	-
Eucnecosum brunnescens Sahlb.	+	+	+	+
Eucnecosum tenue (LeC.)	+	+	+	+
Eucnecosum spp.	+	+	+	+
Unamis sp.	+	+	-	-
Phlaeopterus cf. *filicornis* Csy.	+	-	-	-
Phlaeopterus spp.	+	-	-	-
Olophrum consimile Gyll.	+	+	+	+
Olophrum rotundicolle Sahlb.	+	-	+	+
Olophrum spp.	+	+	+	+
Acidota crenata Fab.	+	-	-	-
Acidota quadrata (Zett.)	+	+	+	+
Geodromicus sp.	-	-	-	+
Hapalarea sp.	+	+	-	+
Stenus dissentiens Csy.	+	-	-	+
Stenus sibiricus Sahlb.	+	-	-	-
Stenus vexatus Csy.	-	-	+	-
Stenus (*Colonus*) sp.	-	-	-	+
Stenus sp.	+	+	+	-
Lathrobium sp.	+	+	-	-
Philonthus sp.	+	+	+	-
Quedius molochinoides Smet.	-	-	+	-
or *lanei* Htch.	-	-	+	-
Quedius (*Raphirus*) sp.	-	-	+	-
Quedius sp.	+	+	+	+
Lordithon sp.	+	+	+	-
Tachinus angustatus Horn	+	-	-	-
Tachinus consortus Hatch	+	-	-	-
Tachinus elongatus Gyll.	+	-	-	-
Tachinus spp.	+	-	-	-
Tachyporus borealis Campbl.	+	-	-	-
Tachyporus borealis or *nimbicola* Campbl.	+	-	-	-
Tachyporus sp.	+	+	-	+
Aleocharinae genus indet.	+	+	+	-
Genus indet.	+	-	-	+
Leiodidae				
cf. *Hydnobius* sp.	+	-	-	-
Genus indet.	-	+	+	-
Scarabaedidae				
Aegialia lacustris LeC.	+	+	-	-
Aphodius wickhami Brown	+	+	-	-
Aphodius sp.	-	-	+	+
Byrrhidae				
Simplocaria sp.	+	-	-	-

List of Arthropod Taxa from Four Holocene Sites in the Colorado Front Range

Taxon	Lake Isabelle Delta Site	Lake Isabelle Peat Site	Lefthand Reservoir	Mt. Ida Ridge Pond
Cytilus sp.	+	-	-	-
Curimopsis grisea LeC.	+	-	-	-
Dryopidae				
Helichus sp.	+	-	-	-
Elmidae				
Genus indet.	+	-	-	-
Elateridae				
Ampedus sp.	+	-	-	-
Limonius sp.	+	-	-	-
Ctenicera resplendens (Esch.)	+	-	-	-
cf. *Ctenicera* sp.	+	-	-	-
Negastrius sp.	+	-	-	-
Genus indet.	+	-	-	+
Cantharidae				
Podabrus (*Lateralis*) sp.	+	-	-	-
Podabrus sp.	-	-	+	-
Anobiidae				
Genus indet.	+	-	-	-
Bostrichidae				
Stephanopachys sobrinus Csy.	+	+	+	-
Cleridae				
Genus indet.	+	-	-	-
Nitidulidae				
cf. *Carpophilus* sp.	+	-	-	-
Epurea sp.	+	-	-	-
Cucujidae				
Laemophloeus sp.	+	-	-	-
Coccinellidae				
Hyperaspis quadrivittata LeC.	+	-	+	-
Hippodamia convergens Guer.	+	-	-	-
Lathridiidae				
Corticaria sp.	-	-	+	-
Genus idet.	+	-	-	+
Colydiidae				
Lasconotus sp.	+	+	-	-
Mycetophagidae				
Genus indet.	+	-	-	-

List of Arthropod Taxa from Four Holocene Sites in the Colorado Front Range

Taxon	Lake Isabelle Delta Site	Lake Isabelle Peat Site	Lefthand Reservoir	Mt. Ida Ridge Pond
Cerambycidae				
Monochamus scutellatus (Say)	+	-	-	-
Genus indet.	+	-	-	-
Chrysomelidae				
Plateumaris flavipes (Kby.)	-	-	+	+
Graphops cf. *wyomingensis* Blake	+	-	+	-
Pyrrhalta sp.	+	-	-	-
Altica spp.	+	+	+	+
Hispinae genus indet.	+	-	-	-
Genus indet.	-	-	-	+
Curculionidae				
Apion sp.	+	+	-	+
Pissodes strobi (Peck)	+	-	-	-
Magdalis lecontei Horn	+	-	-	-
Rhyncolus brunneus Mannh.	+	-	-	-
Rhyncolus macrops Buch	+	+	+	-
Cossonus sp	+	-	-	-
Genera indet.	+	+	-	-
Scolytidae				
Scolytus piceae Sw.	+	+	-	-
Scierus annectans LeC.	+	-	-	-
Scierus pubescens Sw.	-	-	+	-
Xylechinus montanus Blkm.	+	-	-	-
cf. *Xylechinus* sp.	+	-	-	-
Hylastes cf. *gracilis* LeC.	+	-	-	-
cf. *Hylastes* sp.	+	-	-	-
Dendroctonus rufipennis (Kby.)	+	+	-	-
Dendroctonus sp.	+	-	+	+
Phloeotribus lecontei Schedl.	+	+	+	-
Carphoborus cf. *carri* Sw.	+	-	-	-
Carphoborus sp.	+	-	-	-
Polygraphus rufipennis (Kby.)	+	+	+	+
Cryphalus ruficollis Hopk.	+	-	-	-
cf. *Trypodendron* sp.				
Trypophloeus striatulatus (Mann.)	+	-	-	-
Dryocoetes affaber (Mannh.)	+	-	-	-
Dryocoetes cf. *autographus* (Ratz.)	+	-	-	-
cf. *Dryocoetes* sp.	+	-	-	-
Pityokteines minutus Say	+	-	-	+
Pityokteines sp.	+	-	-	-
Orthotomicus caelatus (Eich.)	+	-	-	-
Conophthorus sp.	+	-	-	-
Pityophthorus spp.	+	+	+	+
Genus indet.	-	+	-	+
HETEROPTERA				
Lygaeidae				
Genus indet.	+	+	+	+

List of Arthropod Taxa from Four Holocene Sites in the Colorado Front Range

Taxon	Lake Isabelle Delta Site	Lake Isabelle Peat Site	Lefthand Reservoir	Mt. Ida Ridge Pond
TRICHOPTERA				
Limnephilidae				
Genera indet.	+	+	+	+
Phryganeidae				
Agrypnia sp.	-	-	+	-
HYMENOPTERA				
Formicidae	+	+	-	-
Camponotus cf. *herculeanus* L.	+	-	-	-
Formica neorufibarbis Whlr.	+	-	-	-
Formica fusca subaenescens Emery	-	-	+	-
Formica sp.	-	-	+	-
Myrmica cf. *detritinodis* Emery	+	-	-	-
Myrmica cf. *lobifrons* Perg.	+	-	-	-
Dolichoderus taschenbergi Mayr	+	-	-	-
Leptothorax sp.	-	-	+	+
Hymenoptera parasitica				
Genera indet.	+	+	+	+
ARACHNIDA				
Aranaeae				
Genus indet.	+	-	+	+
ACARI				
Oribatidae				
Genus indet.	+	+	+	+
CRUSTACEA				
CLADOCERA				
Daphnia spp.	-	-	+	+

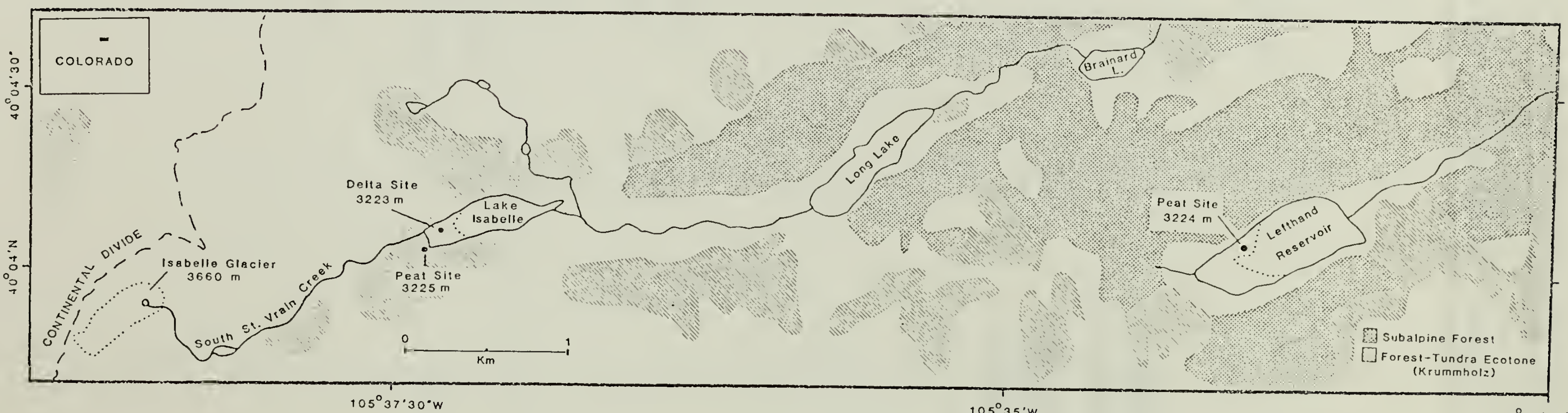

COLORADO
CONTINENTAL DIVIDE
Isabelle Glacier
3660 m
South St. Vrain Creek
Delta Site
3223 m
Lake
Isabelle
Peat Site
3225 m
0
1
Km
Long Lake
Brainard
L.
Peat Site
3224 m
Lefthand
Reservoir
Subalpine Forest
Forest-Tundra Ecotone
(Krummholz)
40°04'30"
40°04'N
105°37'30"W
105°35'W
105°32'30"W

Fig. 1

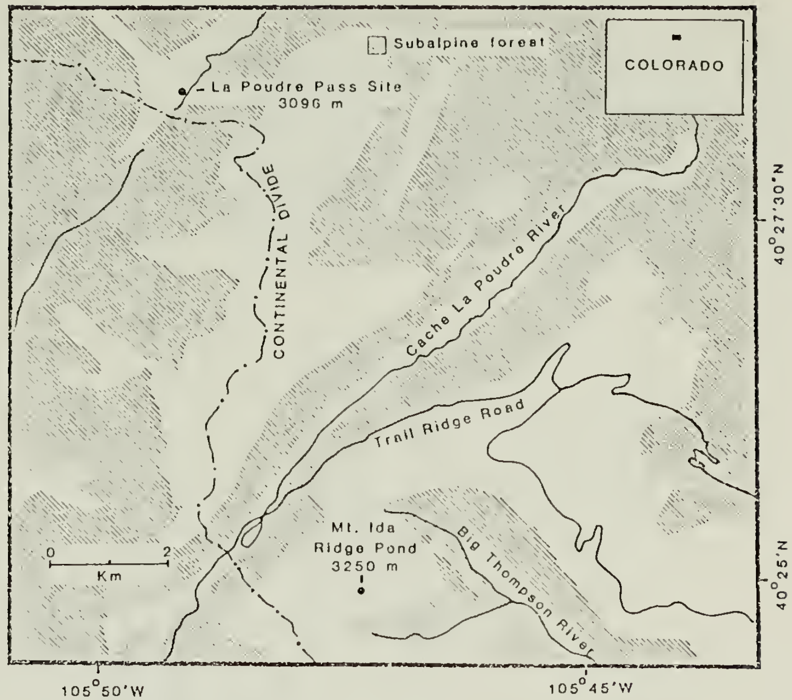

Subalpine forest
COLORADO
La Poudre Pass Site
3096 m
CONTINENTAL DIVIDE
Cache La Poudre River
Trail Ridge Road
Mt. Ida
Ridge Pond
3250 m
Big Thompson River
0
2
Km
40°27'30"N
40°25'N
105°50'W
105°45'W

Fig. 2

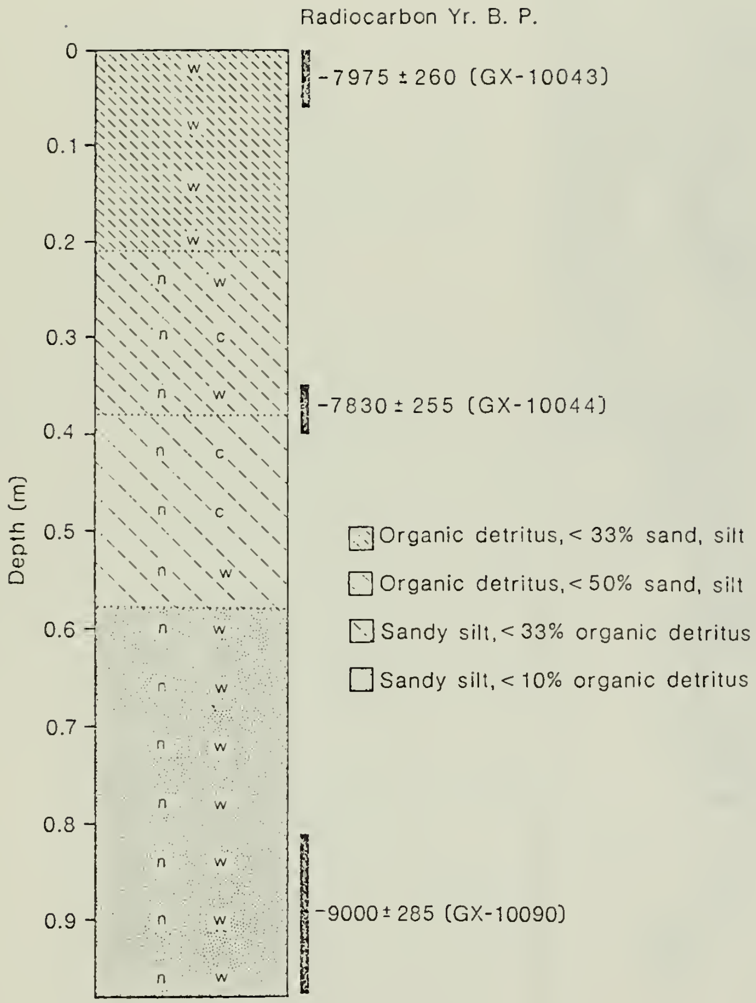

Radiocarbon Yr. B. P.
-7975 ± 260 (GX-10043)
-7830 ± 255 (GX-10044)
-9000 ± 285 (GX-10090)
Depth (m)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Organic detritus, < 33% sand, silt
Organic detritus, < 50% sand, silt
Sandy silt, < 33% organic detritus
Sandy silt, < 10% organic detritus

Fig. 3

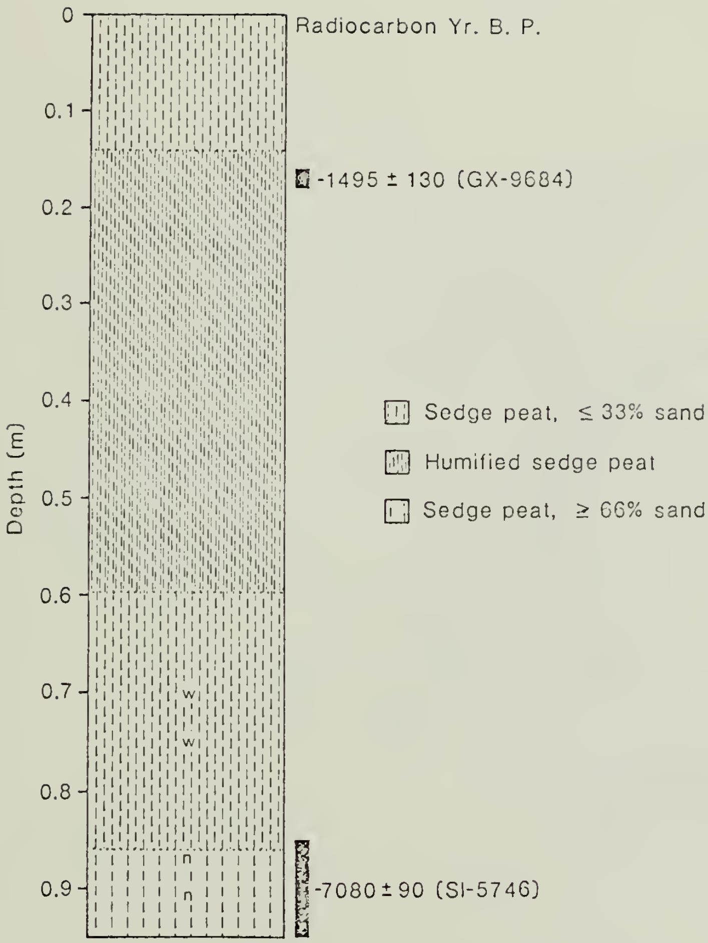

0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Depth (m)
Radiocarbon Yr. B. P.
-1495 ± 130 (GX-9684)
-7080 ± 90 (SI-5746)
w
w
n
n
Sedge peat, ≤ 33% sand
Humified sedge peat
Sedge peat, ≥ 66% sand

Fig. 4

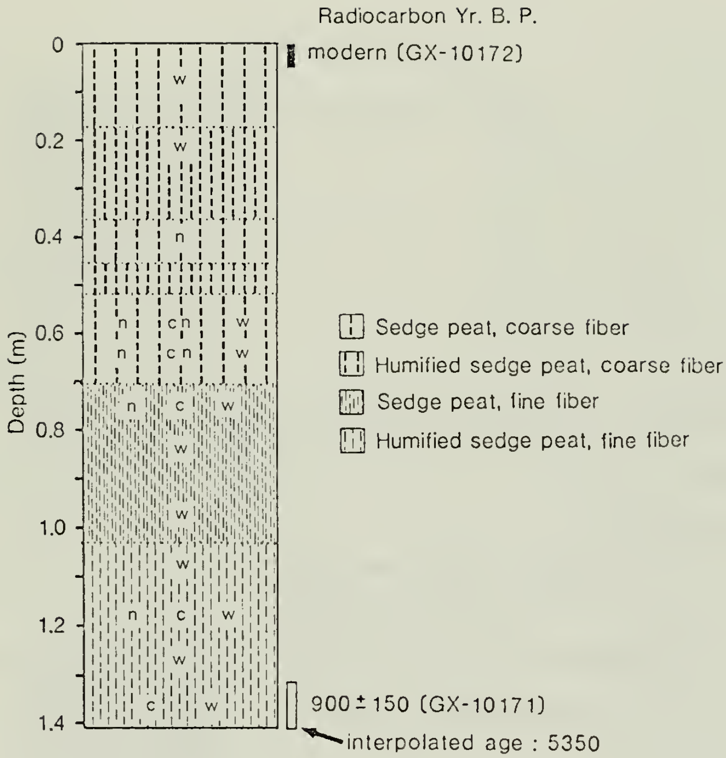

Radiocarbon Yr. B. P.
modern (GX-10172)
900 ± 150 (GX-10171)
interpolated age : 5350
Depth (m)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Sedge peat, coarse fiber
Humified sedge peat, coarse fiber
Sedge peat, fine fiber
Humified sedge peat, fine fiber

Fig. 5

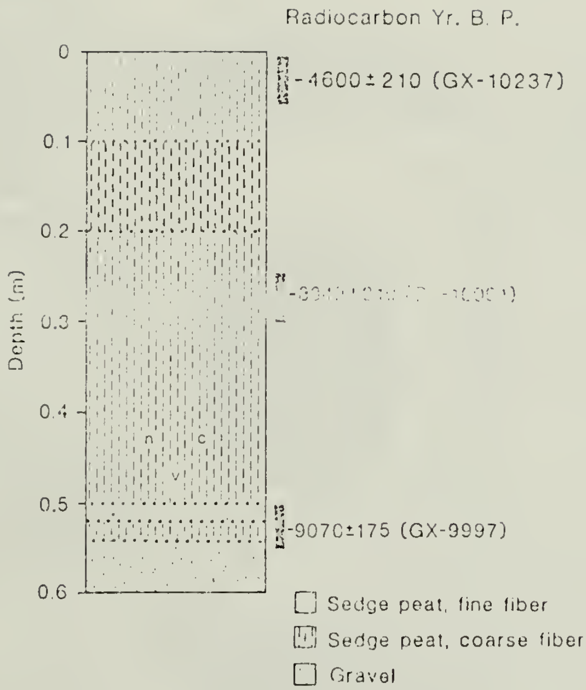

Radiocarbon Yr. B. P.
0
0.1
0.2
0.3
0.4
0.5
0.6
Depth (m)
-4600±210 (GX-10237)
-9070±175 (GX-9997)
Sedge peat, fine fiber
Sedge peat, coarse fiber
Gravel

Fig. 6

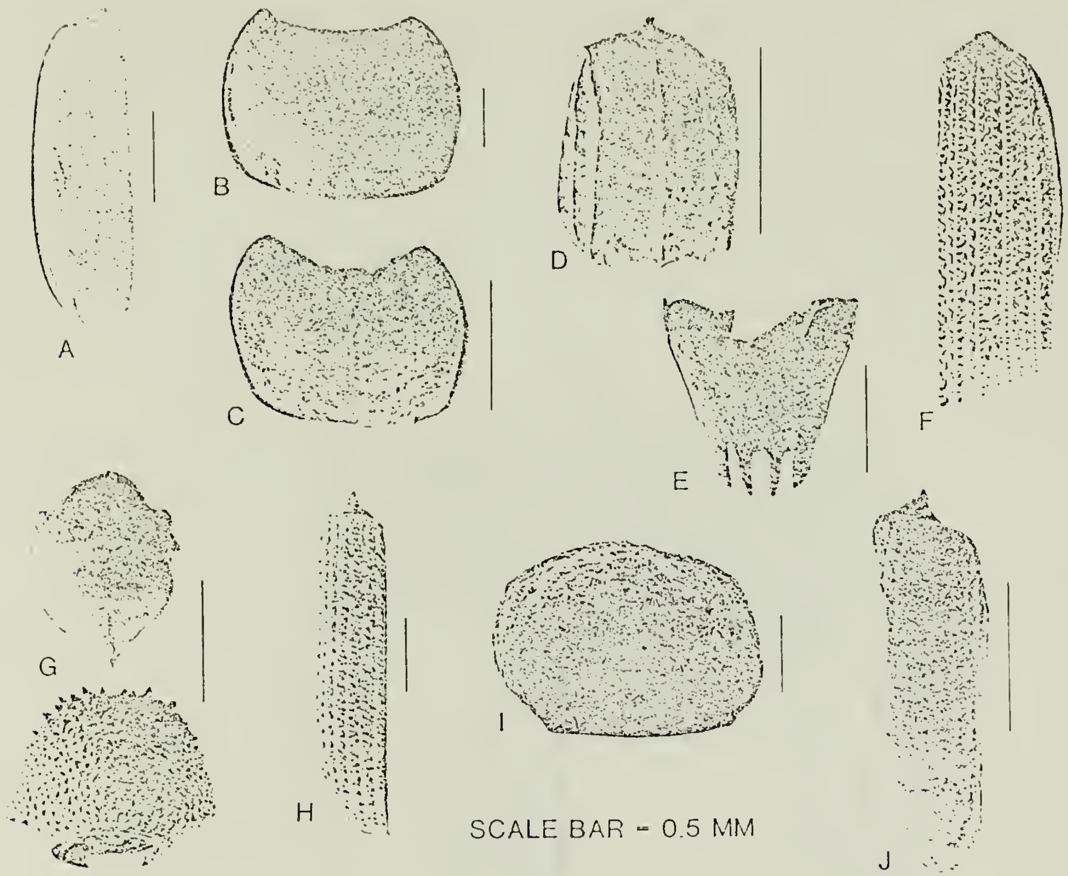
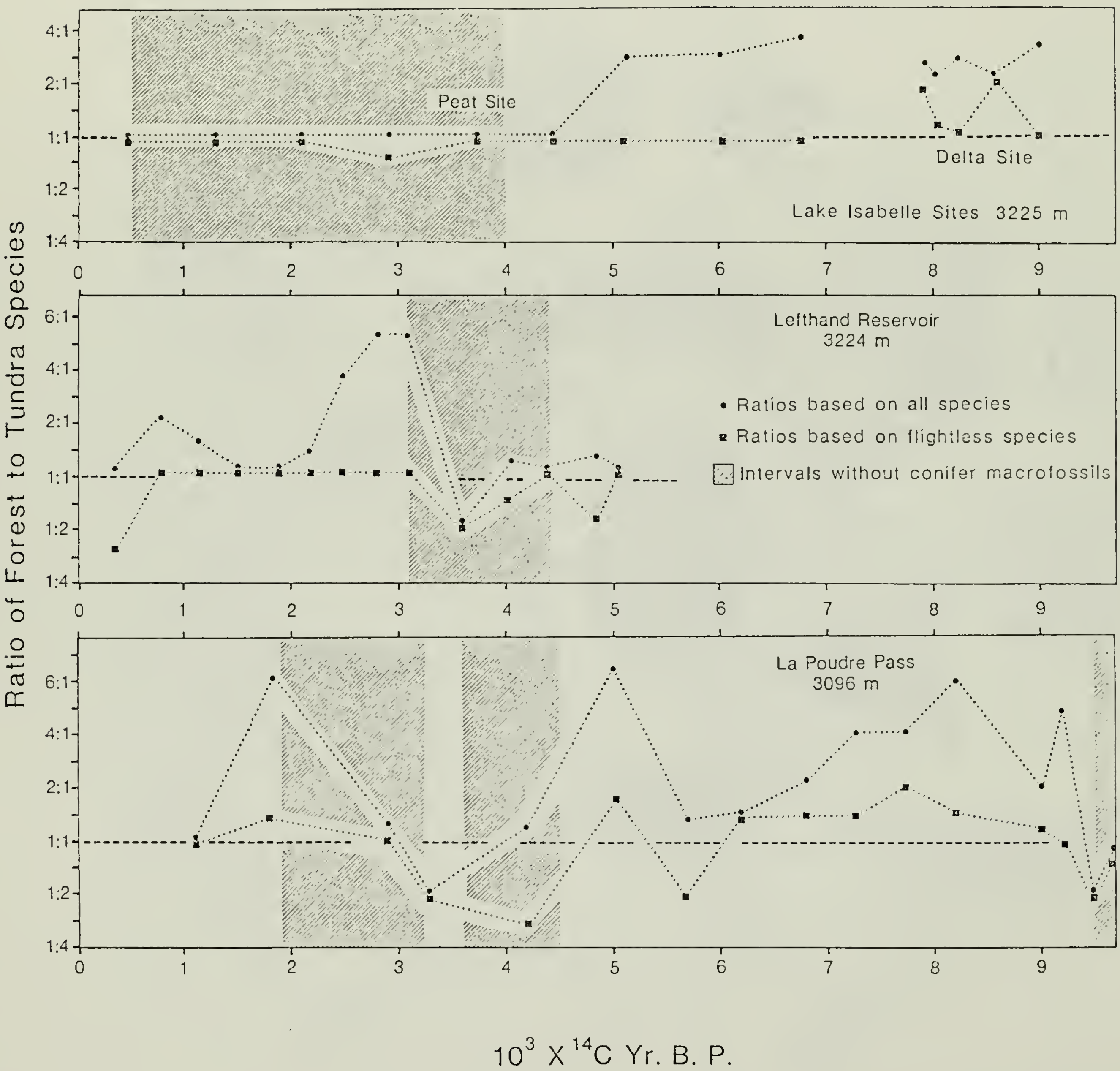


Fig. 7

Fig. 8



Ratio of Forest to Tundra Species
Peat Site
Delta Site
Lake Isabelle Sites 3225 m
Lefthand Reservoir
3224 m
• Ratios based on all species
Ratios based on flightless species
Intervals without conifer macrofossils
La Poudre Pass
3096 m
4:1
2:1
1:1
1:2
1:4
6:1
0
1
2
3
4
5
6
7
8
9
10³ X ¹⁴C Yr. B. P.

Fig. 9

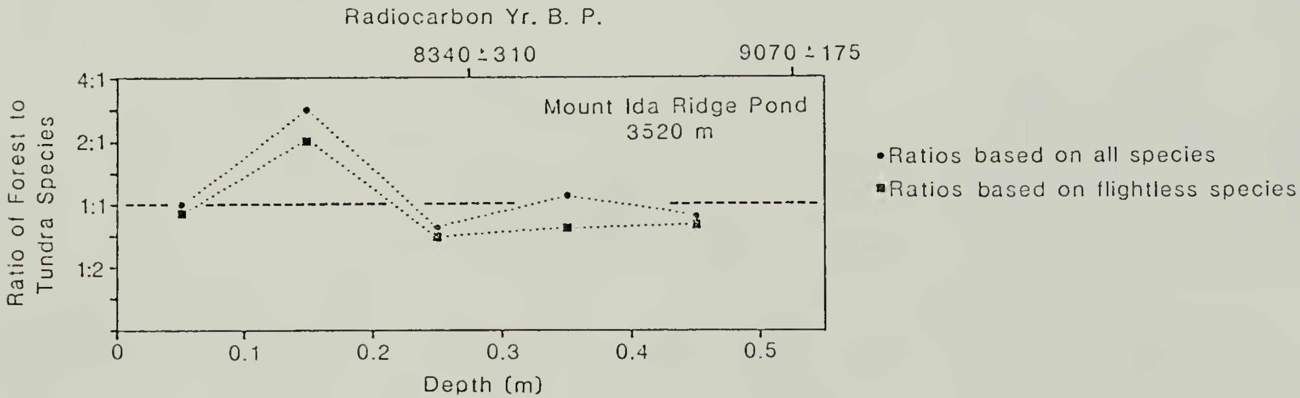
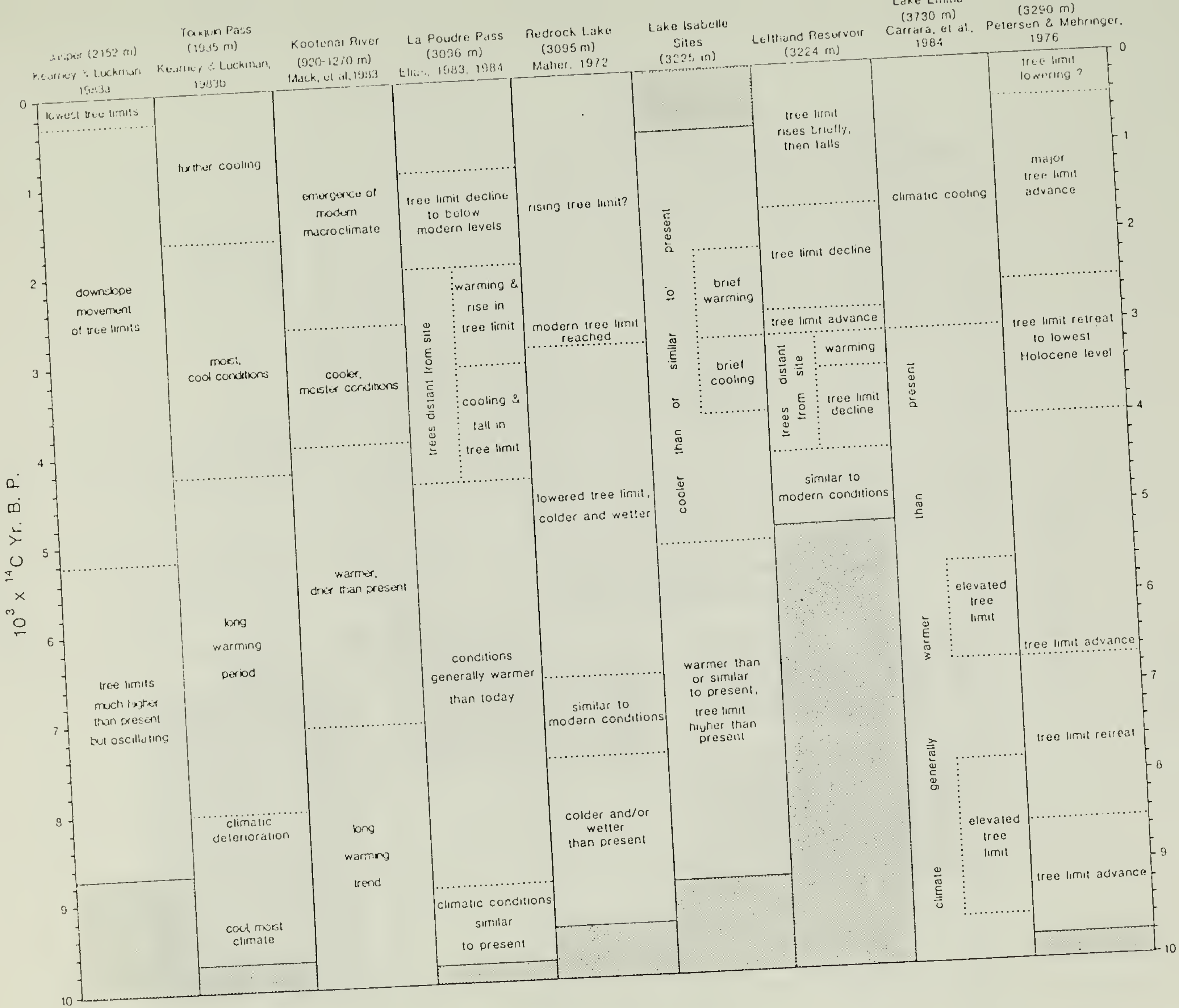

Radiocarbon Yr. B. P.
8340 ± 310
9070 ± 175
Mount Ida Ridge Pond
3520 m
Ratio of Forest to Tundra Species
4:1
2:1
1:1
1:2
0
0.1
0.2
0.3
0.4
0.5
Depth (m)
•Ratios based on all species
▪Ratios based on flightless species

Fig. 10



$10^3 \times {}^{14}C$ Yr. B. P.
Jasper (2152 m) Kearney & Luckman 1983a
Tonquin Pass (1935 m) Kearney & Luckman, 1983b
Kootenai River (920-1270 m) Mack, et al, 1983
La Poudre Pass (3096 m) Elias, 1983, 1984
Redrock Lake (3095 m) Maher, 1972
Lake Isabelle Sites (3225 m)
Lefthand Reservoir (3224 m)
(3730 m) Carrara, et al. 1984
(3290 m) Petersen & Mehringer, 1976
lowest tree limits
downslope movement of tree limits
tree limits much higher than present but oscillating
further cooling
moist, cool conditions
long warming period
climatic deterioration
cool, moist climate
emergence of modern macroclimate
cooler, moister conditions
warmer, drier than present
long warming trend
tree limit decline to below modern levels
warming & rise in tree limit
cooling & fall in tree limit
trees distant from site
conditions generally warmer than today
climatic conditions similar to present
rising tree limit?
modern tree limit reached
lowered tree limit, colder and wetter
similar to modern conditions
colder and/or wetter than present
cooler than or similar to present
brief warming
brief cooling
warmer than or similar to present, tree limit higher than present
tree limit rises briefly, then falls
tree limit decline
tree limit advance
warming
trees distant from site
tree limit decline
similar to modern conditions
climatic cooling
climate generally warmer than present
elevated tree limit
elevated tree limit
tree limit lowering ?
major tree limit advance
tree limit retreat to lowest Holocene level
tree limit advance
tree limit retreat
tree limit advance
0
1
2
3
4
5
6
7
8
9
10

Fig. 11